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ON THE TAXONOMIC STATUS OF *ERIOGONUM ROBUSTUM* (POLYGONACEAE), A RARE ENDEMIC IN WESTERN NEVADA

Kristin F. Kuyper[1,2], Ulla Yandell[3], and Robert S. Nowak[1,4]

ABSTRACT.—Evidence from the morphology, genetics, and biogeography of a rare endemic from western Nevada, *Eriogonum robustum*, is presented to determine its most accurate taxonomic classification. Previous authors have classified *E. robustum* Greene both as a species and as a variety of *E. lobbii* Torrey & Gray. However, results of a morphometric comparison for 9 characters establish that significant morphological differentiation exists between *E. robustum* and *E. lobbii*. In addition, results of a genetic study using protein electrophoresis indicate that genetic differentiation may exist between these 2 taxa. Furthermore, the 2 taxa are geographically, ecologically, and reproductively isolated. Finally, the selective pressures that act on *E. robustum* in a narrowly restricted cold-desert environment are different from those that act on *E. lobbii* in a subalpine environment. Thus, all available data support a species-level taxonomic classification for *E. robustum*.

Key words: Eriogonum robustum, Eriogonum lobbii, *morphological differentiation, genetic differentiation, protein electrophoresis, biogeography, endemic species, altered andesite soils.*

Eriogonum Michx. (Polygonaceae) is a large and widespread genus of approximately 240 species. Members of the genus occur mainly in western North America from northern Mexico to Alaska, although some taxa range eastward to the Appalachian Mountains and peninsular Florida (Reveal 1989). The origin of the genus as a whole is unknown, but Reveal (1969) speculated it originated during the Tertiary in an arid or semiarid portion of western North America. Reveal further speculated that subgenera arose at various times and in different geographical areas. Some members of the genus exhibit an ability to colonize new and unstable habitats in dry climates, which results in many geographically restricted taxa (Barneby 1989).

The large number of taxa, a complex evolutionary history, and geographic isolation of many taxa make the taxonomy of the genus a puzzle that challenges those who study *Eriogonum* (Howell 1975). The genus was first described by A. Michaux (1803), and early classifications (Bentham 1837, 1856, Torrey and Gray 1870, Watson 1877, 1879) differed in the number of taxonomic categories as well as assignment of groupings by subgenera or by sections (Myatt 1968). The taxonomy of the genus was last revised by Reveal (1969), who

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recognized 8 subgenera: *Eucycla, Clastomyelon, Micrantha, Eriogonum, Oligogonum, Pterogonum, Ganysma,* and *Oregonium.*

The taxon *Eriogonum robustum* Greene, "andesite buckwheat," is one of the perplexing taxonomic challenges in the genus. *Eriogonum robustum* is a narrowly restricted endemic that occurs on "islands" of hydrothermally altered andesite in the vicinity of Reno, Nevada (Fig. 1). The classification of *E. robustum* in the literature is riddled with inconsistency (Table 1): *Eriogonum robustum* has been classified both as a species and as a variety of *E. lobbii.* The species *E. lobbii* was first described by Torrey and Gray (1870), and their description of its range included the area that populations of *E. robustum* currently occupy. However, in 1885, Greene recognized *E. robustum* as a very local species. He also recognized similarities between *E. robustum* and *E. lobbii* and placed the new species "between *E. compositum* and *E. lobbii.*" However, Jones (1903) reclassified *E. robustum* as *E. lobbii* var. *robustum.* In her revision of the genus, Stokes (1936) agreed with Jones; because *E. robustum* is more robust than *E. lobbii,* she stated that *E. robustum* "is doubtfully even a variety, for superior nourishment would account for the differences." However, Billings (1950, 1992) considered *E. robustum* a "good species" and referred to it as such. He pointed out that the substrate on which *E. robustum* is naturally found (i.e., islands of altered andesite) is low in nutrients, and thus "superior nourishment" could not account for the large size of *E. robustum.* The classification of *E. robustum* as a variety or as a species is not the only inconsistency: the spelling of the variety epithet also varies. For example, Munz (1968) referred to the plant as *E. lobbii* var. *robustius*; Reveal (1985a) used another spelling, *E. robustium.* The correct orthography is *robustum.* For convenience, we reference *E. robustum* as a distinct species in this paper.

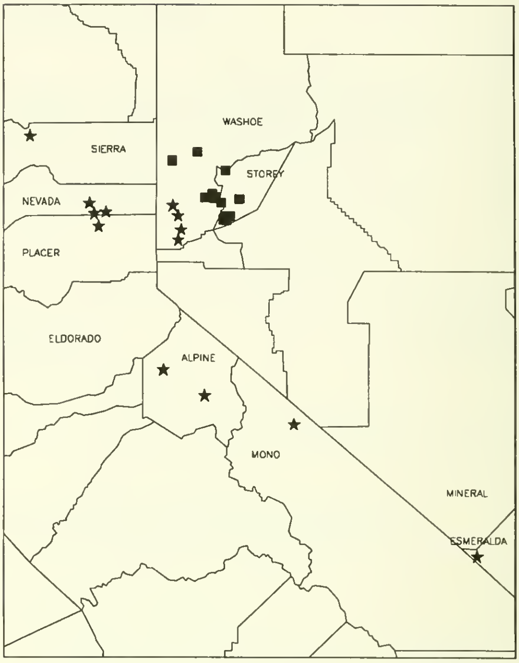

Fig. 1. Locations of *Eriogonum robustum* populations (boxes) and the nearest populations of *E. lobbii* (stars) in west central Nevada and east central California (locations from the Nevada Natural Heritage Program 1994 database and personal observations).

The purpose of this study was to assess the taxonomic classification of *Eriogonum robustum* by investigating the extent to which it and *E. lobbii* differ. The criteria for determining whether or not 2 taxa are separate species depend on the species concept applied. Species concepts generally fall into 4 categories (Slobodchikoff 1976): typological, biological, selective, and evolutionary. The typological concept of species differentiation is based solely on morphological distinctness; i.e., a species is a group of organisms that are more similar morphologically to other individuals within the group than they are to any other group. The biological species concept is based on reproductive isolation between groups of organisms. According to this concept, a species is a group of individuals or natural populations that interbreed but are reproductively isolated from other groups. Under the selection concept, a species is a system of genetically similar individuals. Genetic identity is maintained as a cohesive unit by a set of selective pressures that balance the disruptive forces imposed by environmental factors, mutation, and genetic recombination. Finally, the evolutionary species concept defines species as a spatio-temporal lineage of populations that evolve separately from other lineages and occupy their own ecological niche. In this paper we utilize information from a comprehensive literature review, data from our morphological measurements and from a limited

TABLE 1. Chronology of references to *Eriogonum robustum* in the literature.

Date	Author	Taxonomy
1870	Torrey, J., and A. Gray	*Eriogonum lobbii*
1885	Greene, E. L.	*Eriogonum robustum*
1903	Jones, M. E.	*Eriogonum lobbii* var. *robustum*
1925	Tidestrom, I.	*Eriogonum robustum*
1936	Stokes, S.	*Eriogonum lobbii* var. *robustum*
1950	Billings, W. D.	*Eriogonum robustum*
1968	Munz, P. A.	*Eriogonum lobbii* var. *robustius*
1975	Howell, J. T.	*Eriogonum robustum*
1980	Mozingo, H., and M. Williams	*Eriogonum lobbii* var. *robustum*
1985a	Reveal, J. L.	*Eriogonum robustium*
1985b	Reveal, J. L.	*Eriogonum lobbii* var. *robustum*
1987	Kartez, J. T.	*Eriogonum lobbii* var. *robustum*
1989	Reveal, J. L.	*Eriogonum lobbii* var. *robustum*
1992	Billings, W. D.	*Eriogonum robustum*
1992	Northern Nevada Native Plant Society	*Eriogonum lobbii* var. *robustum*
1992	Morefield, J., and T. Knight (eds.)	*Eriogonum robustum*

electrophoretic study, and observations over 4 growing seasons to assess the most appropriate taxonomic classification of *E. robustum* within the framework of these different species concepts.

MATERIALS AND METHODS

Morphological Analyses

Eighty-three dried herbarium specimens of *Eriogonum robustum* and 383 specimens of *E. lobbii* were examined. The specimens were located at the University of Nevada, Reno, herbarium (RENO) or loaned by 1 of the following herbaria: Bailey Hortorium (BH including CU), Natural History Museum (BM), Brigham Young University (BYU), California State University, Chico (CHSC), University of the Pacific (CPH), University of California, Davis (DAV), Field Museum of Natural History (F), Harvard University Herbaria (GH), University of Idaho (ID), University of California, Berkeley (JEPS), Missouri Botanical Garden (MO), Nevada State Museum (NSM), California Polytechnic State University (OBI), USDA Forest Service, Region 4, Ogden (OGDF), Pacific Union College (PUA), Rancho Santa Ana Botanic Garden (RSA), Santa Barbara Botanic Garden (SBBG), San Jose State University (SJSU), Smithsonian Institution (US), University of California, Berkeley (UC), University of Nevada, Las Vegas (UNLV), and Utah State University (UTC).

One qualitative and 8 quantitative character traits were chosen for morphological analyses. The qualitative trait was umbel structure: simple versus compound. The quantitative characters were petiole length, lamina length, lamina width, involucre length, flowering stem length, flowering stem width, bract length, and bract width. These characters were chosen because of reported differences for those traits and the feasibility of measuring them from herbarium specimens. Petiole length was measured from the point of its attachment on the caudex to the base of the lamina. Lamina length was measured from the base to the tip. Lamina width was measured at the widest point of the leaf. Involucre length was the distance from the point of its attachment on the ray to the tip of the middle lobe. Flowering stem length was measured from its point of attachment on the caudex to the first series of bracts subtending the umbel. Flowering stem width was measured 4 cm below the bracts. Bract length was measured from the point of attachment on the flowering stem to the tip of the bract. Bract width was measured at the widest point of the bract. For the quantitative characters, 3 replicate measurements of each character were made on every plant specimen. These replicate measurements were then averaged to derive the sample measurement for each individual herbarium specimen.

A rankit plot and the Wilt-Shapiro statistic were use to examine normality of the data for each of the 8 quantitative characteristics. The rankit plots were nearly linear and the approximate Wilt-Shapiro statistics were between 0.90 and 0.99, indicating that the data did not deviate greatly from normality. Because sample variances were often not equal among sample populations, nonparametric statistics were used to compare means. A Mann-Whitney (2-sample rank sum) test was conducted for each quantitative character to determine if a mean value for *Eriogonum lobbii* was significantly different from that for *E. robustum*. A Kruskal-Wallis one-way analysis of variance with mean comparison was used to compare the 3 sample populations: *E. lobbii* with simple umbels, *E. lobbii* with compound umbels, and *E. robustum* (which uniformly had compound umbels). In addition, a principal components analysis (PCA) was performed on the 8 quantitative variables to order the specimens in multidimensional space. Pearson's correlations were computed for all 8 quantitative characteristics and the PCA values from axes 1 and 2; tests of significance for the correlation coefficients followed procedures given in Sokal and Rohlf (1981). STATISTX Version 4.1 (Analytical Software, Tallahassee, FL) was used for the nonparametric tests and Pearson's correlations, and PC-ORD Version 2.0 (MjM Software Design, Gleneden Beach, OR) was used for the PCA analysis.

Protein Electrophoresis

Protein electrophoresis was used to determine the extent of genetic divergence between *Eriogonum lobbii* and *E. robustum* using *E. caespitosum* as an outgroup. Fresh, young leaf material was collected in July and August 1993. Leaves were then ground in liquid nitrogen and the samples mixed with the grinding buffer of Bayer and Minish (1993). We were able to resolve 7–8 putative loci, most of them (phosphoglucose isomerase, E.C. 5.3.1.9; gluconate dehydrogenase, E.C. 1.4.1.2; diaphorase, E.C. 1.8.1.4; superoxide dismutase, E.C. 1.15.1.1) on a modified version of the Poulik (1957) discontinuous tris-citrate buffer system (gel buffer: 0.003 M citric acid, 0.015 M tris; electrode buffer: 0.1 M sodium hydroxide, 0.3 M boric acid; Schuster et al. 1989) utilizing horizontal gel electrophoresis. The histidine II buffer system (buffer #18) of King and Dancik (1983) resolved hexoseaminase (E.C. 3.2.1.52) at pH 7.0 and resolved at least 1 distinguishable locus of malate dehydrogenase (E.C. 1.1.1.37), possibly 2, at pH 8.0. Although these methods were repeated for fresh leaf material collected in 1994, no distinct banding patterns occurred during electrophoresis and we were not able to resolve any loci.

RESULTS AND DISCUSSION

Morphological Differentiation

For plants growing in their natural habitat, *Eriogonum robustum* has features that distinguish it from *E. lobbii* and all other buckwheats (Billings 1950 and personal communication, Morefield personal communication, Mozingo and Williams 1980). *Eriogonum lobbii* is a small, low-spreading form, whereas *E. robustum* is a larger, more robust form, as its name implies. Published descriptions of the plants differ in growth form, leaf characters (size and pubescence), and floral form (inflorescence habit, umbel structure, and color; Table 2).

Significant differences existed between *Eriogonum robustum* and *E. lobbii* for all 8 quantitative characters that we measured (Table 3). For all characters except flowering stem length, *E. robustum* had a larger mean than *E. lobbii* (Fig. 2). The differences in character size between *E. robustum* and *E. lobbii* were large for flowering stem width and bract width, where the means for *E. robustum* were, respectively,

TABLE 2. Morphological comparison of *Eriogonum robustum* and *E. lobbii* (Mozingo and Williams 1980, Kartez 1987, Barneby 1989, Reveal 1989, Hickman 1993).

Character	*Eriogonum lobbii*	*Eriogonum robustum*
Growth form	Seldom branched near base Height: 0.3–1.5 dm Width: 0.5–4.0 dm	Much branched near base Height: 1.0–3.0 dm Width: 1.0–3.5 dm
Leaves	Tomentose on lower surface Length: 1.0–5.0 cm	Tomentose entirely Length: 2.5–5.0 cm
Peduncle	Decumbent, branched near tip Length: 6–20 cm	Erect, mostly unbranched Length: 18 cm
Umbels	Simple, sometimes compound Ray #: 2–6 Flower color: cream to yellow aging red	Compound Ray #: 15 Flower color: cream to yellow

TABLE 3. *P* values from Mann-Whitney tests and from Kruskal-Wallis one-way analyses of variance for 8 quantitative characters measured on *Eriogonum lobbii* and *E. robustum* herbarium specimens. For the Kruskal-Wallis analyses, significant differences between means for a particular character are indicated by different letters; units for all means are mm.

Comparison	Petiole length	Lamina length	Lamina width	Involucre length	Flowering stem length	Flowering stem width	Bract length	Bract width
All *E. lobbii* vs. *E. robustum* (Mann-Whitney)	<0.001	<0.001	<0.001	<0.001	0.036	<0.001	<0.001	<0.001
E. lobbii with simple umbels vs. *E. lobbii* with compound umbels vs. *E. robustum* (Kruskal-Wallis AOV)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
K-W mean comparisons:								
E. lobbii, simple umbels	16.6a	21.9a	15.5a	7.7a	89.5a	1.0a	10.8a	2.8a
E. lobbii, compound umbels	22.2b	29.0b	21.2b	8.9b	105.5b	1.3b	14.9b	4.3b
E. robustum	21.7b	31.9b	21.2b	9.1b	82.5a	2.0c	17.7c	4.9c

100% and 60% greater than those for *E. lobbii*, but small for flowering stem length and involucre length, where the means for *E. robustum* were 10% smaller and 15% greater than those for *E. lobbii*. Ranges in character size overlapped for all characters, but the extent of overlap for 95th percentiles was small for flowering stem width and for bract length.

The 2 taxa formed nearly distinct clusters when plotted in the 2-dimensional space of axis 1 and axis 2 from the PCA of the 8 quantitative characters (Fig. 3). *Eriogonum robustum* occurred primarily on the left side of axis 1 and on the lower part of axis 2. *Eriogonum lobbii* occurred primarily on the upper part of axis 2, with the subset of *E. lobbii* with compound umbels primarily on the left side of axis 1 and the subset of *E. lobbii* with simple umbels on the right side of axis 1. PCA axis 1 accounted for 71% of the total variance and axis 2 for 11%. Lamina length, bract length, and lamina width were most highly correlated with axis 1 (Table 4). Flowering stem length, flowering stem width, and petiole length were the 3 characters most highly correlated with axis 2. All correlations were significant with the exceptions of lamina length, lamina width, and involucre length with respect to axis 2 (Table 4).

The frequency of simple and compound umbels differed between taxa (Table 5). One hundred percent of *Eriogonum robustum* had compound umbels, whereas only 16% of *E. lobbii* did. Segregation of the character was significant between taxa as determined by a chi-square test. A one-way analysis of variance was performed to determine how the quantitative morphological characteristics of the subset of *E. lobbii* with compound umbels compared with those of the more typical *E. lobbii* and with those of *E. robustum*. Significant differences existed between the smaller subset of *E. lobbii* and *E. robustum* for 4 of the 8 characters measured. The 2 subsets of *E. lobbii* differed significantly for all 8 characters (Table 3).

In summary, results of the morphological comparison of the 2 taxa show that a significant amount of morphological differentiation exists between *Eriogonum robustum* and *E. lobbii*. Significant differences between the 2 taxa occurred in all 8 quantitative as well as in the 1 qualitative character measured. Principal components analysis separated the samples into nearly discrete groups that corresponded with taxonomy. Despite significant differences in morphological characteristics, construction of a dichotomous key to separate the 2 taxa is difficult, especially a key to use on herbarium specimens. Clearly, if the specimen has simple umbels, then it is *E. lobbii*. However, specimens with compound umbels can be either taxon; for these specimens, flowering stem length and flowering stem width appear to be the best characteristics to differentiate the taxa. Both characters were significantly different between *E. lobbii* with compound umbels and *E. robustum*, and they were most highly correlated with PCA axis 2, which was the PCA axis that separated this *E. lobbii* subset from *E. robustum*. The mean flowering stem length for herbarium specimens of *E. lobbii* with compound umbels was 105 mm (95% CI of 98–113), and that of *E. robustum* was 83 mm (95% CI of 77–88); mean flowering stem width of *E. lobbii* with compound umbels was 1.3 mm (95%

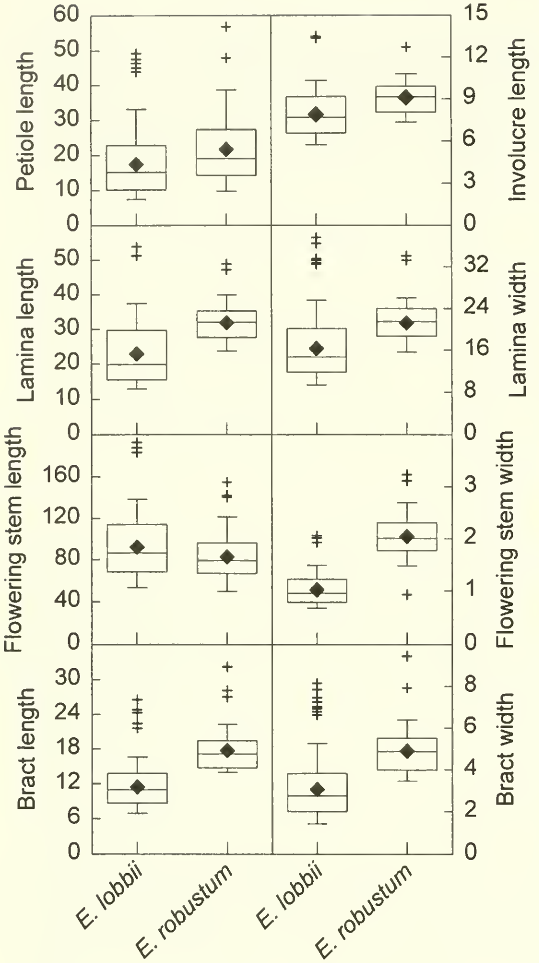

Fig. 2. Box plots for 8 quantitative morphological characters of 383 *Eriogonum lobbii* and 83 *E. robustum* herbarium specimens; units for all measurements are mm. Filled diamonds represent mean values; horizontal lines near the center of the boxes indicate the median; lower and upper edges of the box represent the 25th and 75th percentiles; error bars below and above the box indicate the 5th and 95th percentiles; the points indicated by a + represent possible outliers.

CI of 1.2–1.4), and that of *E. robustum* was 2.0 mm (95% CI of 1.9–2.1). For specimens without a clear umbel structure, flowering stem length is a less reliable character (Fig. 2), and the larger bract size should be coupled with larger flowering stem width to identify *E. robustum*. The 95% CIs for bract length and width are 17–19 mm and 4.6–5.2 mm, respectively, for *E. robustum* versus 10–11 mm and 2.7–3.0 mm for *E. lobbii* with simple umbels and 14–16 mm and 3.8–4.7 mm for *E. lobbii* with compound umbels. For specimens without an inflorescence, shorter petioles and smaller leaves are diagnostic of *E. lobbii*: petiole length of 16–18 mm, lamina length of 21–23 mm, and lamina width of 15–16 mm correspond with the 95% CI for the subset of *E. lobbii* with simple umbels. Unfortunately, specimens with petiole length >19 mm, lamina length >30 mm, and lamina width >20 mm could be either taxa, as the 95% CIs for these characters overlap for *E. robustum* and for the subset of *E. lobbii* with compound umbels. In the field other characters such as flowering stem growth habit (prostrate or erect), relative density of tomentum on the lamina, and number of rays are also useful.

Reproductive Isolation

The distributions of the 2 taxa do not overlap (Fig. 1). *Eriogonum lobbii* occurs on gravelly, rocky, or clayey slopes and ridges from approximately 1800 to 3650 m in the northern Coast Ranges of California north to southern Oregon and in the Sierra Nevada of California and western Nevada (Reveal 1989). The distribution of *E. robustum* is restricted to altered andesitic soils in the Reno region, ranging from 1310 to 2440 m in elevation (Billings unpublished). As of 1994 there were 15 confirmed populations of *E. robustum* (Nevada Natural Heritage Program personal communication), located in the Virginia Range, on Peavine Mountain, and in Sun Valley north of Reno. Spatial and ecological barriers between populations of *E. robustum* and *E. lobbii* likely formed during the climatic changes since the late Pleistocene (Billings 1950, DeLucia and Schlesinger 1990).

Not only are *Eriogonum robustum* and *E. lobbii* geographically isolated, but the nearest interspecific populations are separated by distances that are large relative to the expected dispersal potential of both taxa. In addition, the taxa are largely seasonally isolated due to the elevation differences in their ranges. *Eriogonum robustum* flowers in March through August; *E. lobbii* flowers in July through September (NNNPS 1992).

Geographical, seasonal, and ecological isolation prevent genetic exchange, which can eventually lead to reproductive isolation and the formation of distinct evolutionary units. Other examples of this pattern in genera with relict populations in Nevada can be found in *Polemonium* (Grant 1989) and *Ipomopsis* (Grant and Wilken 1988). Another result of geographical,

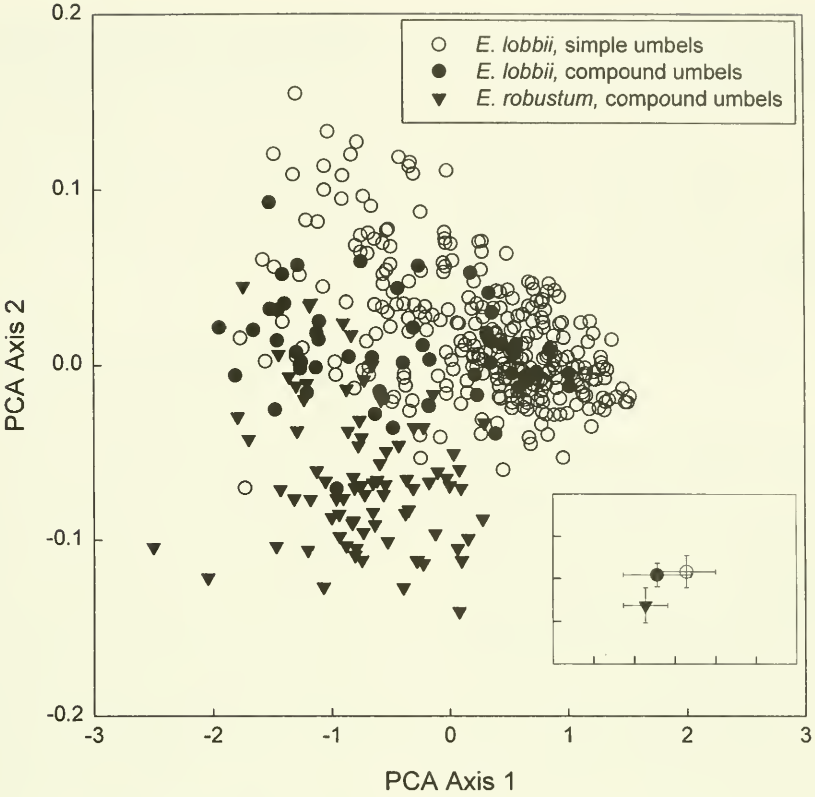

Fig. 3. Principal component analysis of 8 quantitative morphological characters measured from herbarium specimens of *Eriogonum lobbii* and *E. robustum.* Inset: mean and standard deviation of axis 1 and axis 2 values for *E. lobbii* with simple umbels (open circles), *E. lobbii* with compound umbels (filled circles), and *E. robustum* (filled triangles).

seasonal, and ecological isolation can be morphological differentiation.

Genetic Differentiation

A tantalizing pattern appeared in the 1993 electrophoretic trials. An unidentified isozyme, diagnostic to species, appeared on system 26 for the following enzyme stains: aspartate aminotransferase (E.C. 2.6.1.1), phosphoglucose isomerase, and gluconate dehydrogenase. The bands of the unidentified isozyme moved farthest in *Eriogonum robustum* samples, 0.9 as far for *E. lobbii,* and were absent for *E. caespitosum.* A pattern of this sort suggests a possible genetic marker differentiating all 3 taxa. However, sample sizes were very small (4 *E. lobbii*, 5 *E. caespitosum*, and 10 *E. robustum* individuals) with only 1 population of each taxa sampled. Thus, although it is an unlikely occurrence, we cannot absolutely rule out the possibility that these markers are population-specific rather than species-specific.

We attempted to replicate and expand the electrophoretic survey in 1994 but were unable to resolve the same enzyme systems that year. Because the late winter and spring of 1994 were much drier than the corresponding periods in 1993, we suspect that the plants had modified their physiology enough to alter the electrophoretic results, possibly by changing the ratio of the amounts of active enzymatic proteins to secondary compounds, which in turn inhibits electrophoretic resolution. We had also conducted electrophoretic trials with different buffers for leaves collected in October 1992, but none of these trials were successful.

Evolutionary Divergence

Eriogonum robustum and *E. lobbii* are both placed in the subgenus *Oligogonum* Nutt. (Reveal 1969). *Oligogonum* includes 32 species in 7 sections that are widely distributed throughout most of western North America with 1 disjunct species in the Appalachian Mountains.

TABLE 4. Pearson's correlation coefficients between each of the 8 morphological characters and scores from axis 1 and axis 2 of the principal components analysis. *P* values for the test of significance are given in parentheses.

Character	Axis 1	Axis 2
Petiole length	–0.806 (<0.001)	0.384 (<0.001)
Lamina length	–0.950 (<0.001)	0.038 (0.431)
Lamina width	–0.910 (<0.001)	0.006 (0.906)
Involucre length	–0.784 (<0.001)	–0.040 (0.407)
Flowering stem length	–0.671 (<0.001)	0.656 (<0.001)
Flowering stem width	–0.813 (<0.001)	–0.417 (<0.001)
Bract length	–0.916 (<0.001)	–0.232 (<0.001)
Bract width	–0.878 (<0.001)	–0.236 (<0.001)

TABLE 5. Number of herbarium specimens with simple and compound umbel structure for 367 *Eriogonum lobbii* and 83 *E. robustum* specimens; 16 specimens had no umbel.

	Umbel structure	
Species	Simple	Compound
Eriogonum lobbii	309	58
Eriogonum robustum	0	83

Reveal (1989) hypothesized that the species within the subgenus *Oligogonum* evolved in 3 geographical areas: the Rocky Mountains, southeastern Oregon and adjacent Idaho, and California. The species in the 3rd center were ultimately derived from species that originated in the 2nd center and had migrated south. Several isolated endemics, including *E. robustum*, have been produced from this 3rd center of origin.

The fact that *Eriogonum robustum* is often classified as a variety of *E. lobbii* strongly suggests that they are closely related taxa. Stokes (1936) grouped species based on their inferred geographic movements from glacial times until the present. According to her biogeographical treatment of the genus, *E. lobbii* and its closest relatives, *E. latens* and *E. compositum*, migrated southward and southeastward along the eastern Sierra Nevada from the northwest Great Basin (Idaho and Oregon) during glacial advances. Some species in this group "descended from the mountains during the course of migration, and now occur in isolated patches on the mountains of the Basin and upon mountains to the south." Thus, Stokes postulates that *E. robustum* simply represents remnant populations of *E. lobbii* and does not warrant taxonomic status at the species level. Alternatively, the 2 species may have differentiated much earlier, with *E. robustum* better adapted either to more arid conditions of the Great Basin or to the low nutrient availability of altered andesite soils. Unfortunately, neither taxon is present in the local fossil record for the last 30,000 years (Nowak et al. 1994a, 1994b), so direct evidence to differentiate between these hypotheses is not available. However, under the origin hypothesis in which *E. lobbii* is the progenitor of *E. robustum*, the critical issue is not when the 2 taxa diverged, but whether the 2 taxa evolved sufficient differences such that they now occupy different ecological niches. Because *E. robustum* has few populations that occur within a relatively small range and are restricted to a single edaphic condition, it is likely that all *E. robustum* populations have evolved under the same selective pressures. The selective pressures that act on *E. robustum* in a nutrient-poor, cold-desert environment are likely different from those that act on *E. lobbii* in a subalpine environment. Thus, the criteria for evolutionary divergence appear to be met. We note that genetic drift can also affect the direction of differentiation between 2 taxa following isolation; thus, we cannot assume that the unique characteristics of *E. robustum* are adaptive and improve its fitness. However, when determining whether 2 taxa are distinct species, differentiation does not have to be adaptive, but simply maintained.

CONCLUSIONS

Although the previous taxonomic treatments of *Eriogonum robustum* vary nearly evenly between the ranks of variety and species, the available evidence is uniformly consistent with a species ranking. Results of this study are consistent with most requirements for the various species concepts discussed above. First, *E. robustum* has morphological characteristics that differentiate it from *E. lobbii* uniformly throughout its range. Second, results of electrophoresis indicate that genetic differentiation may exist: a genetic marker is present that distinguishes the 2 taxa. Third, although we do not have direct evidence that the taxa are reproductively isolated, circumstantial evidence strongly indicates reproductive isolation. Geographical, seasonal, and ecological isolation can result in reproductive isolation, and morphological and genetic differentiation can be a product of reproductive isolation. Finally, populations of *E. robustum* have likely evolved under the same selective pressures at least since the end of the Pleistocene, and those pressures are almost certainly different from those acting on *E. lobbii*. Because the exchange of genetic material has been interrupted by geographical isolation, *E. robustum* and *E. lobbii* can be expected to maintain the significant degree of morphological differentiation that currently exists as well as continue to diverge as they are selected for different climatic and edaphic conditions.

Eriogonum lobbii exhibits a compound umbel structure sporadically throughout its range, unlike *E. robustum* that uniformly has compound umbels. The occurrence of a compound umbel structure in *E. lobbii* does not appear to be correlated with location or elevation. The presence of this expression in *E. lobbii* raises 2 possibilities: (1) the subset of *E. lobbii* with compound umbels represents an intermediate form between the 2 taxa; or (2) umbel form is simply variable in *E. lobbii*. Unfortunately, our data cannot differentiate between these possibilities. For example, the subset of *E. lobbii* with compound umbels differed from the subset of *E. lobbii* with simple umbels for all 8 morphological characters, but differed from *E. robustum* for only 4 of the characters (Table 3), which suggests that the subset of *E. lobbii* with compound umbels represents an intermediate form. On the other hand, the mean values for PCA axis 1 and axis 2 of both subsets of *E. lobbii* were closer together than the subset of *E. lobbii* with compound umbels and *E. robustum* (inset, Fig. 3), suggesting that the umbel form is simply variable within *E. lobbii*.

Additional evidence is desirable before a definitive conclusion can be drawn. For example, hybridization experiments would establish whether reproductive isolation has been established. Additional genetic studies would also be useful, although based upon our experience, these studies should use techniques other than protein electrophoresis to ensure a greater probability of success. Alternative evidence to establish the presence of genetic differentiation would require that morphological differences be maintained in plants that are grown in a uniform environment, i.e., a "common garden." Billings (personal communication) transplanted several individuals of both taxa into the Duke University phytotron and grew them for a period of approximately 1 yr under uniform climatic conditions. Dr. Billings observed that both taxa maintained their unique morphologies (i.e., growth form, leaf characteristics), but each taxon had been grown in its native soil: *Eriogonum lobbii* in granitic soils and *E. robustum* in altered andesite. Data from a rigorous common garden experiment where both plants are grown under similar climatic and edaphic conditions for 2 or more generations would be necessary to demonstrate the presence or absence of a genetic basis for the existing morphological differences.

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DISTRIBUTION AND ABUNDANCE OF NATIVE BONNEVILLE CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI UTAH*) IN SOUTHWESTERN UTAH

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ABSTRACT.—The Bonneville cutthroat trout (*Oncorhynchus clarki utah*; BCT) was once abundant throughout the Bonneville Basin. In southwestern Utah, however, only 3 local populations of the subspecies were known to exist in 1977, when conservation efforts to protect and replicate them began. By 1995 remnant populations were known in 6 streams, and replicate populations had been established in an additional 16. Populations of BCT in southwestern Utah streams were surveyed by electrofishing in 1994 and 1995 to describe the subspecies' status. Estimated densities of age-1 and older BCT ranged from 118 to 546 fish per km. Biomass estimates ranged from 8 to 64 kg per ha. Several age groups of BCT were collected at most locations. Six populations were classified as self-sustaining, 9 as expanding through natural recruitment, 6 as new, and 1 as hybridized. Overall status of BCT in southwestern Utah has improved since 1977, but conservation measures must continue to maintain a positive trend.

Key words: cutthroat trout, native, southwestern Utah, distribution, abundance, management, Sevier River, Beaver River, Virgin River.

The Bonneville cutthroat trout (*Oncorhynchus clarki utah*; hereafter BCT) is the only trout native to the Great Basin in Utah. Within the eastern portion of the Great Basin, this subspecies once occupied ancient Lake Bonneville and was abundant in waters throughout the Bonneville Basin. Numbers of BCT rapidly declined in the late 1800s and early 1900s as a result of habitat modifications, introduction of nonnative fishes, and overharvest (Cope 1955, Duff 1988, Behnke 1992). Widespread introductions of rainbow trout (*Onchorhynchus mykiss*) and Yellowstone cutthroat trout (*O. c. bouvieri*), in particular, displaced native trout from much of their former range. By 1955 it was feared that the native BCT might be extinct (Cope 1955). Behnke (1976), however, reported that a few remnant populations still existed in isolated streams in remote locations, 3 of which were in southwestern Utah: Birch Creek, a small headwater stream in the Beaver River drainage, and Reservoir and Water canyons in the Virgin River drainage. The Virgin River is part of the lower Colorado River basin and lies immediately south of the Bonneville Basin. It was uncertain whether these 2 populations were natural or introduced by early settlers (Behnke 1976, 1992). The southwestern Utah populations were restricted to <8 km of stream in 1977.

In the mid-1970s, the Bureau of Land Management developed habitat improvement plans for Birch Creek, and the U.S. Fish and Wildlife Service considered the BCT for federal listing under the Endangered Species Act (Bureau of Land Management 1976). Shortly thereafter, several additional remnant populations of BCT were reported from the Intermountain West (Hickman and Duff 1978). By 1988, 40 populations of BCT were recognized in Utah, Wyoming, and Idaho (Duff 1988).

In Utah the Division of Wildlife Resources (UDWR) began efforts to expand the range of BCT in 1977 by replicating the Birch Creek population. BCT from Birch Creek eventually were replicated in 4 additional streams. Other remnant populations from southwestern Utah were discovered in Deep Creek (Behnke 1976, Martin and Shiozawa 1982), the North Fork of North Creek (Martin and Shiozawa 1982), and Ranch Creek (this report and D. K. Shiozawa, Brigham Young University, personal communication). Populations from Reservoir and Water canyons were each replicated in 3 streams. A mixed population from Water and Reservoir canyons was established in Leeds Creek and 1 of its tributaries, Pig Creek. A mixed population from Reservoir Canyon, Water Canyon, and Birch Creek was established in Pine Creek. Fish from Pine Creek were subsequently introduced into Manning Meadow Reservoir to create a BCT broodstock, primarily for sport fishery management. By 1995 remnant populations of BCT were known from 6 southwestern Utah streams, and replicate populations were established in 8 other areas (Fig. 1).

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Our objective is to describe the current status of "conservation populations" of BCT in southwestern Utah, defined as those which are managed to ensure the continued existence of native subspecies (Schmidt et al. 1995). Population status was described by summarizing recent data on distribution, abundance, and population structure for all known conservation populations of BCT in the Sevier, Beaver, and Virgin river drainages. Comparisons were made between recent and older survey data to describe population changes or trends. A brief review of conservation measures for BCT in southwestern Utah is also provided.

METHODS

Pure populations of BCT were identified by at least 2 independent reviews using different methods: meristic characteristics along with fish-stocking records, electrophoresis, and mitochondrial DNA analysis (Behnke 1976 and personal communication, Martin and Shiozawa 1982, Martin et al. 1985, Thompson 1987, Shiozawa and Evans 1994a, 1994b).

All known BCT populations in southwestern Utah were sampled during 1994–95 using a backpack electrofisher. Surveys were conducted when stream conditions allowed effective sampling. We avoided periods when flows were high, turbidity made visibility difficult, or streams were partially frozen. A minimum of two 161-m (0.1-mile) stations were electrofished on primary streams (defined as the highest order stream in an area that contained BCT). A minimum of 1 station was electrofished on primary stream tributaries. Stations included habitat representative of the stream or stream section. One electrofishing pass was made through a station, moving upstream, and we attempted to collect all BCT except young-of-the-year (Y-O-Y). Measurements of individual fish lengths (TL) were taken on all BCT collected. Y-O-Y were observed from midsummer through fall and were smaller than about 76 mm (TL). Y-O-Y were noted as present or absent. Also recorded was the number of larger (>76 mm TL) BCT observed but not collected. That number was then added to the number collected to estimate the minimum population of age-1 and older BCT. Previous estimates of minimum population based on 1 pass were similar to population estimates made using the removal method (Zippin 1956).

Individual fish weight was estimated using the relationship

$$\text{Log(Weight)} = -4.91367 + 2.95756\ \text{Log(Length)};$$

the model was based on data from 373 BCT from 6 small streams in southwestern Utah prior to 1994. We tested for significant differences between the populations used to calculate the length/weight model (Dunn and Clark 1974). There was a significant difference between individual regressions, but we used the pooled model to estimate weights and biomass because maximum variation between estimates from pooled and individual regressions was only 2 kg per ha.

A minimum of 10 random stream width measurements (wetted channel) were taken at each station to calculate surface area. Trout standing crop was calculated using mean weights and estimates of minimum population of age-1 and older fish.

We also electrofished outside designated sampling stations to determine the distribution (upstream and downstream range) of BCT in some streams. Reaches where BCT were observed were classified as occupied habitat. Available habitat included occupied areas as well as areas in which we thought BCT would eventually become established. Stream lengths for habitat categories were from U.S. Geological Survey 7.5-minute series topographical maps.

To describe changes and trends in BCT populations, we compared recent abundance and distribution data to past information from UDWR files. We also made some comparisons with data for nonnative rainbow trout at several locations from which they were later removed prior to establishing BCT by transplants. Survey methods used prior to 1994 were similar to those listed above. We made visual observations to supplement formal surveys at some BCT streams and reviewed related work such as collections for transplants.

We assessed the status of each surveyed population using the above data and knowledge of land-management practices and habitat quality in BCT streams. BCT populations were

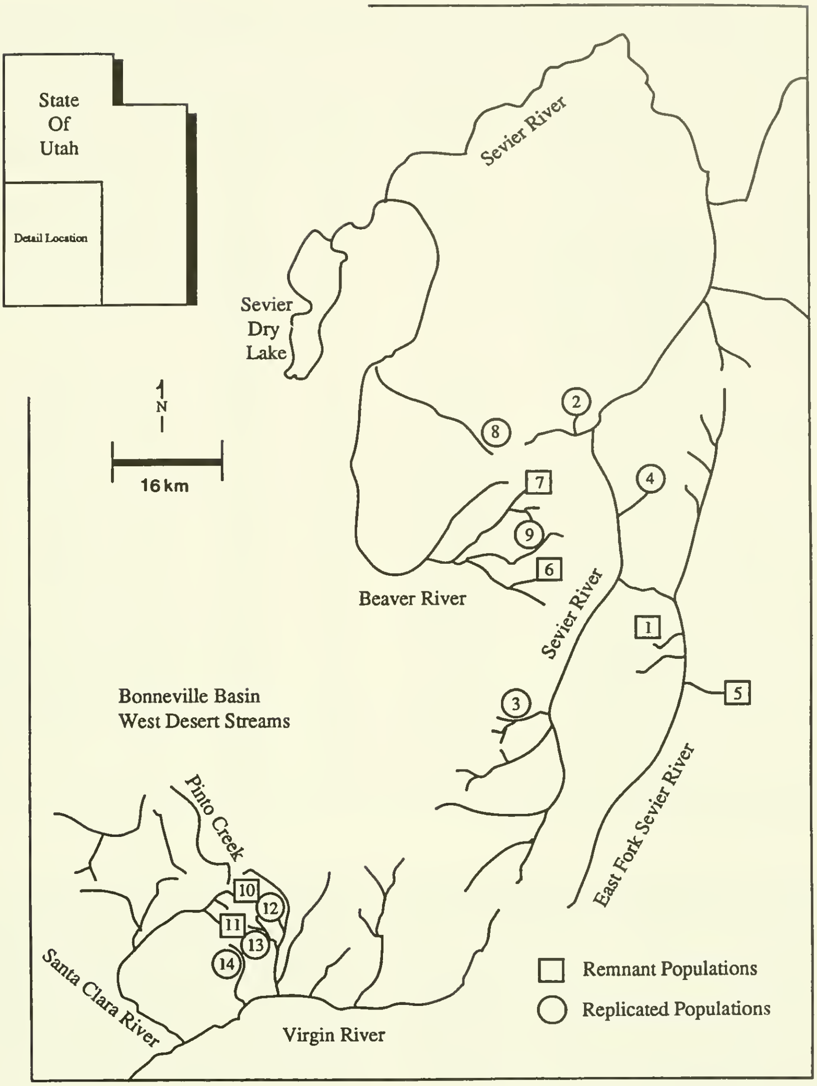

State
Of
Utah
Detail Location
Sevier River
Sevier
Dry
Lake
N
16 km
Beaver River
Sevier River
Bonneville Basin
West Desert Streams
Pinto Creek
East Fork Sevier River
Santa Clara River
Virgin River
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Remnant Populations
Replicated Populations

Fig. 1. Map of the Sevier, Beaver, and Virgin river drainages in southwestern Utah. Reference numbers correspond to primary streams containing Bonneville cutthroat trout populations as listed in Table 4.

classified as self-sustaining, expanding, new, or hybridized. Self-sustaining populations had multiple successive year classes and appeared distributed throughout the suitable habitat available at the time of sampling. Expanding populations showed evidence of natural recruitment but did not occupy all available habitat. Recently established populations were classified as new, and any population that showed evidence of introgression with nonnative trout was considered hybridized.

RESULTS

Estimated densities of age-1 and older BCT ranged from 118 to 546 fish per km (Table 1), and biomass ranged from 8 to 64 kg per ha. Several age groups of BCT were collected at most locations, with older fish ranging up to 305 mm TL (Fig. 2). Most fish collected were 100–250 mm TL. The highest biomass estimates for age-1 and older BCT were for Leed's Creek drainage, where they ranged from 53 to

TABLE 1. Stream lengths and abundance of Bonneville cutthroat trout in southwestern Utah, 1994–95.

					Trout abundance in occupied habitat			
Primary stream/tributary	Number of stations sampled (number in occupied habitat)	Average stream width (m)	Available km	Occupied km	Number per km	Number per ha	Kg per km	Kg per ha
Deep Creek	2 (2)	1.86	9.7	9.7	276	1484	9.1	49
Sam Stowe Creek[a]	3 (3)	1.43	4.8	4.8	306	2136	14.3	100
Threemile Creek	Introduction in 1994	1.31	8.8	[b]	—	—	—	—
Delong Creek	Introduction in 1994	—	3.4	[b]	—	—	—	—
Indian Hollow	Introduction in 1994	—	1.6	[b]	—	—	—	—
Manning Creek	Treatment in 1995	—	16.4	[b]	—	—	—	—
Barney Outlet	Treatment in 1995	—	2.1	[b]	—	—	—	—
Collins Creek	Treatment in 1995	—	2.1	[b]	—	—	—	—
Vale Creek	Treatment in 1995	—	1.9	[b]	—	—	—	—
Ranch Creek	2 (2)	1.04	11.7	4.5	171	1657	5.5	53
Birch Creek	4 (3)	1.19	8.8	6.8	160	1351	5.0	42
N. Fk. North Creek	6 (2)	2.59	8.8	3.2	214	827	9.2	36
Pole Creek	Introduction in 1995	—	4.3	[b]	—	—	—	—
Pine Creek	3 (3)	1.86	6.3	6.3	228	1225	5.0	27
Briggs Creek	2 (2)	1.55	1.4	1.0	124	797	5.6	36
Reservoir Canyon Creek	2 (2)	2.35	3.2	3.2	546	2336	12.0	51
Water Canyon Creek	3 (1)	1.98	3.2	0.8	118	595	1.7	8
Leap Creek	4 (2)	1.80	8.8	2.7	130	721	5.6	31
South Ash Creek	3 (2)	3.32	6.0	4.0	189	570	8.9	27
Harmon Creek	2 (2)	2.71	4.8	1.8	174	639	8.5	31
Mill Creek	2 (2)	3.11	7.4	5.1	252	807	8.6	27
Leeds Creek	3 (2)	2.71	11.3	4.8	264	973	16.3	60
Pig Creek	1 (1)	1.34	1.6	1.6	230	1723	7.1	53
Spirit Creek	2 (2)	1.46	3.5	1.8	261	1788	9.4	64
Horse Creek	Introduction in 1995	—	3.4	[b]	—	—	—	—

[a] Bonneville cutthroat trout hybridized with rainbow trout.

[b] Limited occupied habitat because fish were recently introduced.

64 kg per ha. The lowest estimate was Water Canyon, where habitat was <1 km during dry years.

BCT densities (trout per km) were higher during recent than past samplings at 4 streams (Table 2). Recent biomass estimates were intermediate between estimates for past years at 2 waters and lower than any previous estimates at 2 of the streams surveyed. Population data were also available for 2 streams that contained rainbow trout prior to BCT introductions (Table 3). Leap Creek had an estimated population of 360 rainbow trout per km in 1983 compared to 304 and 130 BCT per km in 1989 and 1995, respectively. Population estimates for Leeds Creek were 646 rainbow trout per km in 1980 and 193 BCT per km in 1995. Estimates of biomass for these 2 streams were also lower for cutthroat trout populations than for rainbow trout, but mean lengths for cutthroat trout were substantially greater than those recorded for rainbow trout collected earlier.

One population surveyed during 1994–95 was hybridized with rainbow trout. The BCT population in Sam Stowe Creek was established by a transplant from Birch Creek in 1977. Rainbow trout from Clear Creek migrated into Sam Stowe Creek sometime after 1984, the year of the last survey prior to 1995. Barriers that had previously prevented fish movement between Clear Creek and Sam Stowe Creek were removed by highway construction or changes in irrigation diversion structures during the last 10 yr. The hybridized BCT population in Sam Stowe Creek, incidentally, had the highest biomass recorded for any of the trout populations surveyed in 1994–95.

There are currently 57.3 km of occupied and 140.5 km of available stream habitat for BCT in southwestern Utah (Table 1). Of the populations surveyed, we classified 6 as self-sustaining, 9 as expanding, 6 as new, and 1 as hybridized (Table 4).

DISCUSSION

Many factors influenced trout densities in both remnant and transplanted BCT populations. These included habitat quality, which was often determined by land-management

TABLE 2. Current abundance (1994-95) of selected Bonneville cutthroat trout populations in southwestern Utah compared to previous years.

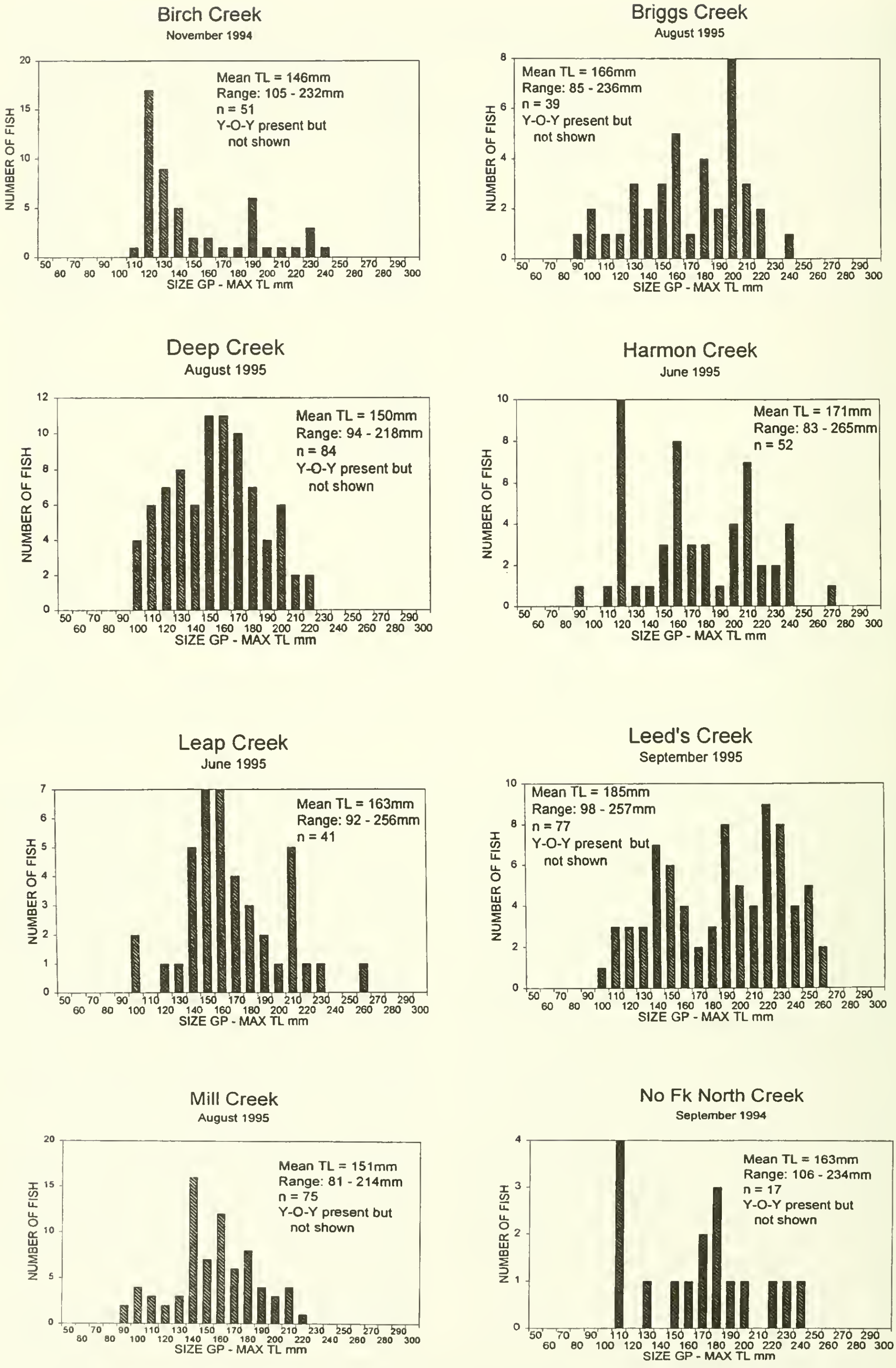
		Number of trout per km (number of survey stations)		
Population (source)	Year	Upper stream	Middle stream	Lower stream
Deep Creek (remnant)	1980	—	161 (1)	—
	1995	—	435 (1)	118 (1)
Birch Creek (remnant)	1970	404 (1)	—	186 (1)
	1974	385 (1)	248 (1)	—
	1975	230 (1)	342 (1)	—
	1980	161 (1)	0 (1)	0 (1)
	1987	—	335 (1)	—
	1994	155 (1)	174 (1)	149 (1)
N. Fk. North Creek (remnant)	1970	273 (1)	—	—
	1981	56 (1)	—	—
	1994	214 (2)	0 (2)	0 (2)
Reservoir Canyon (remnant)	1980	397 (1)	—	—
	1995	540 (1)	553 (1)	—
Water Canyon Creek (remnant)	1980	37 (1)	99 (1)	12 (1)
	1995	118 (1)	0 (1)	0 (1)
Sam Stowe Creek (transplant)	1980	174 (1)	0 (1)	—
	1984	422 (1)	25 (1)	—
	1995[a]	422 (1)	292 (1)	205 (1)
Pine Creek (transplant)	1982	130 (1)	75 (1)	168 (1)
	1984	—	298 (2)	248 (1)
	1994	180 (1)	230 (1)	273 (1)
Leap Creek (transplant)	1989	304 (1)	—	—
	1994	—	0 (1)	0 (2)
	1995	130 (2)	—	—

[a] Bonneville cutthroat trout hybridized with rainbow trout.

practices, and natural events such as droughts, floods, and fires. Many of the streams we surveyed were relatively small and the amount of trout habitat varied considerably with annual variations in stream flow. Much of lower Birch Creek, for example, contained marginal trout habitat that was caused by low flow and high water temperature. Surveys have been conducted 6 times on Birch Creek since 1970 (Table 2). Estimated BCT densities generally exceeded 250 fish per km, with >10 km occupied during extended periods of high water. Following droughts in 1977 and the early 1990s (Utah Climate Center 1994), BCT density was generally <175 fish per km. In 1980 the population was confined to the upper 3 km or less of stream. Changes in land management (Bureau of Land Management 1976) have since improved trout habitat in Birch Creek and reduced impacts of recent drought. Even though the latest drought was more severe and of longer duration than the 1977 drought, a healthy population existed in >6 km of stream.

Effects of drought were even more dramatic at Water Canyon, where surveys were conducted following droughts in 1977, the late 1980s, and early 1990s (Table 2). BCT densities were very low. By late summer 1989, BCT were restricted to <0.5 km of stream near the headwaters; the remainder was completely dry. Good water years occurred during the mid-1980s (Utah Climate Center 1994), and fish expanded into >3 km of stream. Formal surveys were not conducted in the mid-1980s, but we knew by our observations that BCT numbers and range had increased greatly. In fact, we collected and transplanted over 190 BCT from the lower portion of Water Canyon in 1986–1989 to establish replicate populations in Leap, Spirit, and Pig creeks. All BCT collected for transplants were taken from the lower 2 km of stream, which had been dry in 1977. During our 1995 survey BCT were still recovering from the drought that began in 1989 and were restricted to approximately 1 km of stream.

Fires, flash floods, and associated changes in water quality have also impacted BCT streams in southwestern Utah. Summer rainstorms following a 1986 wildfire in the Leeds Creek watershed severely reduced the rainbow trout



Birch Creek
November 1994
Mean TL = 146mm
Range: 105 - 232mm
n = 51
Y-O-Y present but not shown

Briggs Creek
August 1995
Mean TL = 166mm
Range: 85 - 236mm
n = 39
Y-O-Y present but not shown

Deep Creek
August 1995
Mean TL = 150mm
Range: 94 - 218mm
n = 84
Y-O-Y present but not shown

Harmon Creek
June 1995
Mean TL = 171mm
Range: 83 - 265mm
n = 52

Leap Creek
June 1995
Mean TL = 163mm
Range: 92 - 256mm
n = 41

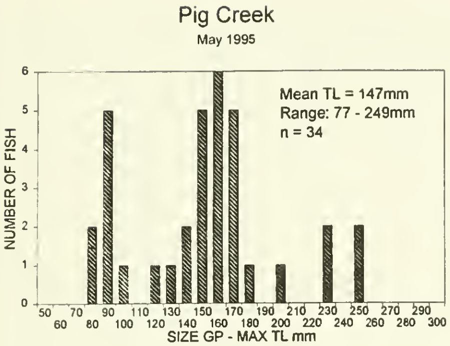
Leed's Creek
September 1995
Mean TL = 185mm
Range: 98 - 257mm
n = 77
Y-O-Y present but not shown

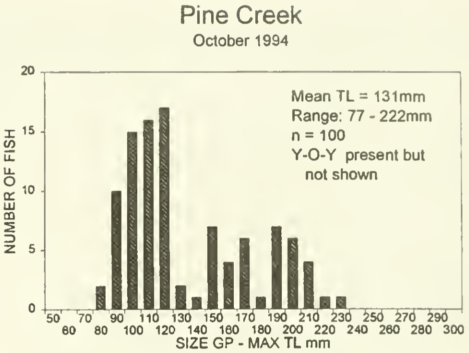
Mill Creek
August 1995
Mean TL = 151mm
Range: 81 - 214mm
n = 75
Y-O-Y present but not shown

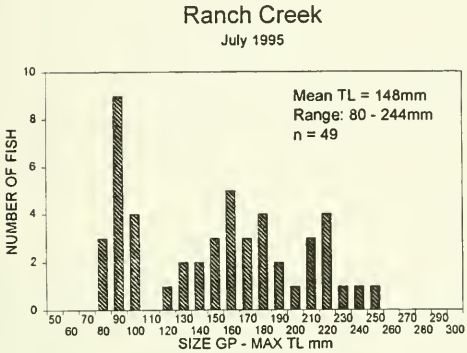
No Fk North Creek
September 1994
Mean TL = 163mm
Range: 106 - 234mm
n = 17
Y-O-Y present but not shown

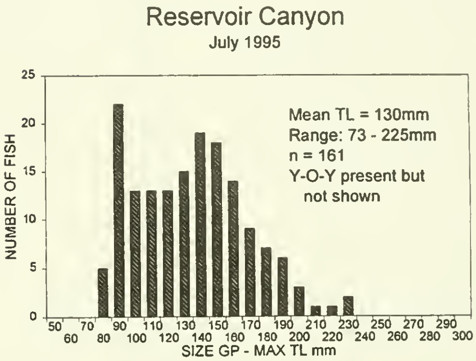
NUMBER OF FISH
SIZE GP - MAX TL mm
50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230 240 250 260 270 280 290 300
0 5 10 15 20
0 2 4 6 8
0 2 4 6 8 10 12
0 2 4 6 8 10
0 1 2 3 4 5 6 7
0 1 2 3 4

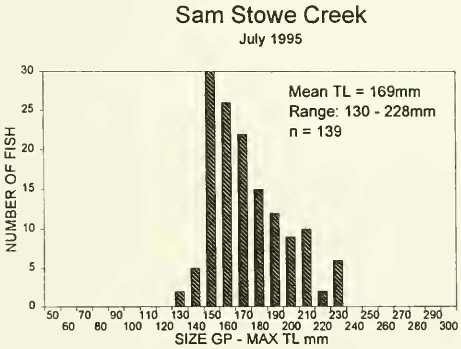
Fig. 2. Frequency histograms of total length measurements (mm) of Bonneville cutthroat trout collected from southwestern Utah streams, 1994–95.

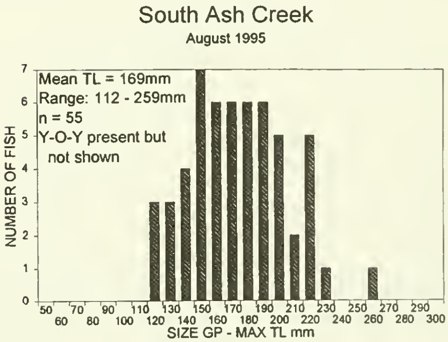


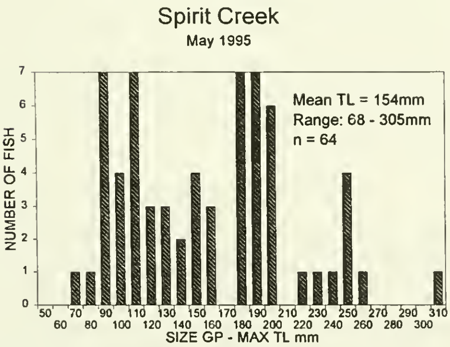












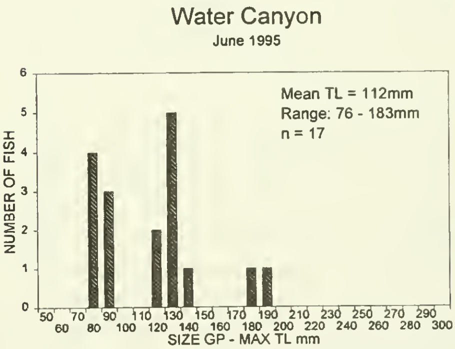


Fig. 2. Continued.

TABLE 3. Abundance, biomass, and total length of Bonneville cutthroat trout and rainbow trout in 2 southwestern Utah streams (samples were from different time periods but from the same survey locations).

Stream	Species/year	Number per km	Kg per km	Mean length (mm)	*n*
Leap Creek	Rainbow trout 1983	360	11.8	130	29
	Cutthroat trout 1989	304	2.5	96	25
	Cutthroat trout 1995	130	5.6	163	41
Leeds Creek	Rainbow trout 1980	646	29.6	152	52
	Cutthroat trout 1995	193	12.4	188	28

population present at that time. The few surviving trout were found in springs and tributaries. Propst et al. (1992) reported a similar phenomenon following fires for Gila trout (*O. gilae*) in small streams in New Mexico. When BCT were introduced into Leeds Creek, they were placed in more of the tributaries and farther upstream in headwater springs to reduce the chance of elimination by a future fire.

Another factor that influenced the density of BCT in replicate populations was the elapsed time between the original transplant and our sampling. Many of the replicate populations were still expanding and probably had not reached carrying capacity. The number of BCT initially introduced into replicate streams and the distribution of introduction sites influenced the rate of population expansion. At Pine Creek, for example, where a relatively large number of fish were introduced at several sites, BCT were abundant throughout the stream within 4 yr. At Sam Stowe Creek, in contrast, where a smaller number of BCT were introduced in the headwaters, BCT were not present in the lower reaches after 7 yr. In all instances where BCT introductions were limited to headwater areas (Sam Stowe, Leap, South Ash, and Leeds creeks), downstream movement was slow, even when larger numbers of fish were transplanted. Within a few years after introduction, fish were abundant near areas of their original release, but they were often absent only a short distance downstream.

Use of short-term studies of fish populations to assess land-management practices or build predictive models has been criticized for a number of reasons. Platts and Nelson (1988) found that trout populations in western streams, including some cutthroat populations in the Great Basin, exhibited large annual fluctuations. House (1995) reported that a wild coastal cutthroat population varied from year to year with no apparent changes in habitat conditions. Although we were limited to a single population estimate for many of the "younger" replicate populations, we had multiple-year estimates of density and biomass for a number of populations. Also, we excluded Y-O-Y trout from our estimates as suggested by House (1995) to eliminate the variation inherent when including that age group, and we did not limit our overall rating of BCT populations to formal survey data (see Methods).

In general, the status of BCT in southwestern Utah has improved since the late 1970s when conservation efforts began. Proposed recovery plans for the greenback cutthroat trout (*O. c. stomias*) from Colorado's east slope included establishing a minimum of 20 populations in 50 km of stream as part of the requirements to remove the subspecies from threatened status under the Endangered Species Act (U.S. Fish and Wildlife Service 1983a). The Gila Trout Recovery Plan is more general, noting that down-listing to threatened would be considered when all known indigenous lineages are replicated in the wild (U.S. Fish and Wildlife Service 1993). The Arizona Trout (Apache Trout) (*O. apache*) Recovery Plan lists the establishment and/or maintenance of 30 discrete, self-sustaining populations as a goal for delisting (U.S. Fish and Wildlife Service 1983b). In comparison, the number of BCT populations present in southwestern Utah, which represents only a portion of that subspecies' current range, is now approaching levels listed as goals in the recovery plans for other western native trouts.

Conservation Measures

Recently, the State of Utah, U.S. Fish and Wildlife Service, U.S. Bureau of Land Management, and U.S. Forest Service have begun to develop a Conservation Agreement and a Conservation and Sportfishing Management Strategy for BCT in Utah. These agreements are

TABLE 4. Status of conservation populations of Bonneville cutthroat trout in southwestern Utah, 1995.

Reference number[a]	Drainage/ primary stream/ tributary	Population origin[b]	Year identified or transplanted	Number transplanted	Status[c]
	Sevier River drainage				
1	Deep Creek	Remnant	1982[e,f]	—	S
2	Sam Stowe Creek	BC	1977	39	H
3	Threemile Creek	BC	1994	113	N
	Delong Creek	BC	1994	30	N
	Indian Hollow	BC	1994	30	N
4	Manning Meadow Reservoir	PC	1990	714	N
5	Ranch Creek	Remnant	1995[g]	—	S
	Beaver River drainage[d]				
6	Birch Creek	Remnant	1973[f]	—	S
7	N. Fk. North Creek	Remnant	1982[e]	—	E
	Pole Creek	NFC	1995	35	N
8	Pine Creek	BC, RC, WC	1980	245	S
9	Briggs Creek	BC	1988	100	E
	Virgin River drainage				
10	Reservoir Canyon Creek	Remnant	1973[f]	—	S
11	Water Canyon Creek	Remnant	1973[f]	—	S
12	Leap Creek	WC	1986	72	E
13	South Ash Creek	RC	1986	0	E
	Harmon Creek	RC	1986	80	E
	Mill Creek	RC	1986	173	E
14	Leeds Creek	RC	1989	90	E
	Pig Creek	RC, WC	1989	60	E
	Spirit Creek	WC	1988	59	E
	Horse Creek	SP	1995	35	N

[a] Numbers refer to locations on Figure 1.

[b] BC = Birch Creek, PC = Pine Creek, NFC = North Fork North Creek, RC = Reservoir Canyon, WC = Water Canyon, SP = Spirit Creek.

[c] S = self-sustaining, E = expanding through natural recruitment, N = new, H = hybridized.

[d] The Beaver River drainage is a major subdrainage within the Sevier River drainage.

[e] Martin and Shiozawa (1982)

[f] Behnke (1976)

[g] Present study

intended to continue the present trends to eliminate threats that would warrant BCT listing as threatened or endangered under the Endangered Species Act. Following is a brief discussion of past, current, and planned conservation measures for BCT in southwestern Utah.

IDENTIFYING ADDITIONAL REMNANT POPULATIONS.—Most sites in which pure populations of BCT might persist in southwestern Utah have been surveyed. A number of remaining potential locations are scheduled to be surveyed in 1996–97. Although it is possible that unknown populations may be discovered, it is unlikely that many more will be found.

HABITAT PROTECTION/ENHANCEMENT.—Habitat protection and enhancement has been an integral part of the conservation work for BCT in southwestern Utah since 1976. Efforts to improve or protect habitat for remnant and replicated BCT populations have included changes in land-management practices (grazing, road closures, etc.), construction of in-stream structures to create trout habitat or stabilize stream channels, and construction of migration barriers to prevent invasion of nonnative trout into waters containing BCT. All but 3 of the BCT streams in southwestern Utah are presently designated for "emphasis on fish habitat improvement" or "intensive riparian" management according to U.S. Forest Service Land and Resource Management Plans, or are located in the Pine Valley Mountains Wilderness Area.

REPLICATING REMNANT POPULATIONS.—Work to replicate remnant BCT populations in southwestern Utah began in 1977 and continues today. Currently, plans for future work include replicating the BCT populations in Deep and Ranch creeks and restoring the hybridized population in Sam Stowe Creek to pure BCT.

CONTROL OF NONNATIVE FISH.—The stocking of nonnative cutthroat trout has been discontinued in the Sevier, Beaver, and Virgin river drainages. Chemical treatments with rotenone and migration barriers have been used to remove and/or restrict the movement of nonnative trout in southwestern Utah BCT streams.

BROODSTOCK DEVELOPMENT/SPORTFISHERY MANAGEMENT.—A wild broodstock of southwestern Utah BCT has been established in Manning Meadow Reservoir, Piute County. In 1996 over 100,000 eggs were collected from this broodstock, which is a mixture of BCT from 3 of the remnant populations in the area. Fish produced from the broodstock are used primarily to maintain sportfishing populations of BCT in southwestern Utah where it is currently impossible to maintain conservation populations because of the presence of nonnative trout and the inability to completely remove them.

ACKNOWLEDGMENTS

Thanks are given to the many individuals who worked on BCT projects in southwestern Utah. B. E. May initiated the restoration program in 1977 and reviewed our manuscript. D. K. Shiozawa reviewed the manuscript and has been instrumental in overall restoration efforts. D. J. Duffield worked on many native cutthroat trout projects in southwestern Utah as both an employee of UDWR and USFS. Funding was provided, in part, by Federal Aid in Fish Restoration Project F-44-R, Utah.

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NATURAL VARIABILITY OF VEGETATION, SOILS, AND PHYSIOGRAPHY IN THE BRISTLECONE PINE FORESTS OF THE ROCKY MOUNTAINS

Brigitte M. Ranne[1], William L. Baker[1], Tom Andrews[2], and Michael G. Ryan[2]

ABSTRACT.—*Pinus aristata* Engelm. forest vegetation in Colorado was studied to determine vegetation composition and the relationship between vegetation and environment. Species percent cover, tree size class, and environmental variables were recorded for 49 plots. Previously collected data for 4 plots from New Mexico were included. Environmental variables included latitude, longitude, elevation, slope, aspect, topographic position, parent material, percent rock cover, mean rock size, litter depth, estimated plot age class, and evidence of anthropogenic disturbance. Soils were analyzed for texture, depth, and percent carbon and nitrogen. *Pinus aristata* foliage was analyzed for percent nitrogen and phosphorus. Direct and indirect gradient analyses (CANOCO) were used to determine environmental factors associated with community composition. Vegetation in *P. aristata* forests is influenced primarily by elevation and soil pH. Substrate, soil texture, topographic position, and geographic location are secondary factors. Six plant associations were identified using cluster analysis (listed in an elevational sequence from low to high): *Pinus aristata / Festuca arizonica* Vasey, *Pinus aristata / Festuca thurberi* Vasey, *Pinus aristata / Juniperus communis* L., *Pinus aristata / Vaccinium myrtilus* L., *Pinus aristata / Ribes montigenum* McClatchie, and *Pinus aristata / Trifolium dasyphyllum* Torr. & Gray.

Key words: bristlecone pine, Rocky Mountains, vegetation, Colorado, gradient analysis, classification.

Managing an ecosystem within its range of natural variability is the best way to maintain diverse, resilient, productive, and healthy ecosystems (Society of American Foresters Task Force 1993, Swanson et al. 1994). (The range of natural variability [RNV] of an ecosystem is the range of variation in composition, structure, and dynamics before the influence of European settlers [Swanson et al. 1994]). Insight into the RNV of forest composition, for example, can be gained by studying stands across a range of environmental variation.

The Rocky Mountain bristlecone pine (*Pinus aristata*) is the longest lived tree in the Rocky Mountains, reaching over 2400 years in age (Brunstein and Yamaguchi 1992), about half the age of the oldest specimen of *Pinus longaeva*, a related bristlecone pine most common in the Great Basin (Ferguson 1968). Studies in Rocky Mountain bristlecone pine forests have focused on dendrochronology and tree population structure (Krebs 1972, LaMarche and Stockton 1974, Baker 1991, 1992, Brunstein and Yamaguchi 1992), but little is known about the range of variability in understory species or how vegetation composition changes with environment. Also, the existing classification is based on relatively few data and little quantitative analysis (DeVelice et al. 1986, Hess and Alexander 1986, Komarkova et al. 1988).

Classification of compositional data can be useful for research, management, and conservation (Pfister and Arno 1980, Alexander 1987). Managers may assume that if a particular site belongs to a vegetation type, it will respond to management similarly to other sites of the same vegetation type. When the objective is to preserve representative sites that span the RNV, classification can help in selecting a reserve system. Gradient analysis is also useful for analyzing the relationship between vegetation and environment (Whittaker 1967).

There are several approaches to classifying mountain vegetation. Many researchers have classified mountain vegetation into elevation-based life zones (Ramaley 1907, Daubenmire 1943, Weber 1965). Another approach is the habitat-typing method, which is based on the assumption that potential climax vegetation is the best reflection of the overall environment. Potential climax vegetation is predicted from stand structure and relative shade tolerances of the trees (Pfister and Arno 1980). However, *P. aristata* does not appear to be a climax species, based on habitat type definitions, because it is not regenerating in forests it dominates (Baker

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1992). Baker (1984) proposed a "natural vegetation" classification of "plant associations" based on the composition and structure of mature examples of vegetation as free as possible from human alterations. This approach is more appropriate for *P. aristata* forests because it eliminates the need for inference about the climax vegetation. The climax vegetation paradigm has been challenged recently (Baker 1995, Cook 1996).

Elevation, soil moisture, soil nutrients, soil texture, topography, disturbance, and latitude influence the species composition and structure of forests in the Rocky Mountains (Peet 1978, 1981, Allen and Peet 1990, Allen et al. 1991, Baker 1992). Higher elevations are associated with decreases in temperature and increases in precipitation and snow depth (Barry 1973). In the Sangre de Cristo Mountains, higher elevations have lower soil pH and percent base saturation and higher total nitrogen than lower elevations (Allen and Peet 1990). Soil moisture, which is associated with topographic position, also significantly affects the vegetation composition, as do soil texture and chemistry (Daubenmire 1943, DeVelice et al. 1986, Peet 1988, Allen and Peet 1990).

In this paper we study the plant species composition of *P. aristata* forests across the range of environments they occupy, then classify these forests and analyze the associated environmental factors influencing their composition.

STUDY AREA

Pinus aristata forests are found in the Front, Mosquito, Sawatch, San Juan, and Sangre de Cristo ranges of Colorado (Fig. 1) and extend into New Mexico in the Sangre de Cristos. These forests grow primarily on dry, steep, south-facing slopes at elevations between 2750 and 3670 m (Baker 1992). Soils are shallow and often skeletal. Convective thunderstorms are the main source of summer precipitation, and cyclonic storms often cause heavy winter snows (Peet 1981). Due to their high elevations, *P. aristata* forests are cool even in summer. In the Front Range mean annual temperatures along a transect from 2195 m to 3750 m ranged from 8.3°C to 3.3°C (Barry 1973). Strong winds of 24–40 km per hour are common in the high-elevation forests of the Front Range (Peet 1981).

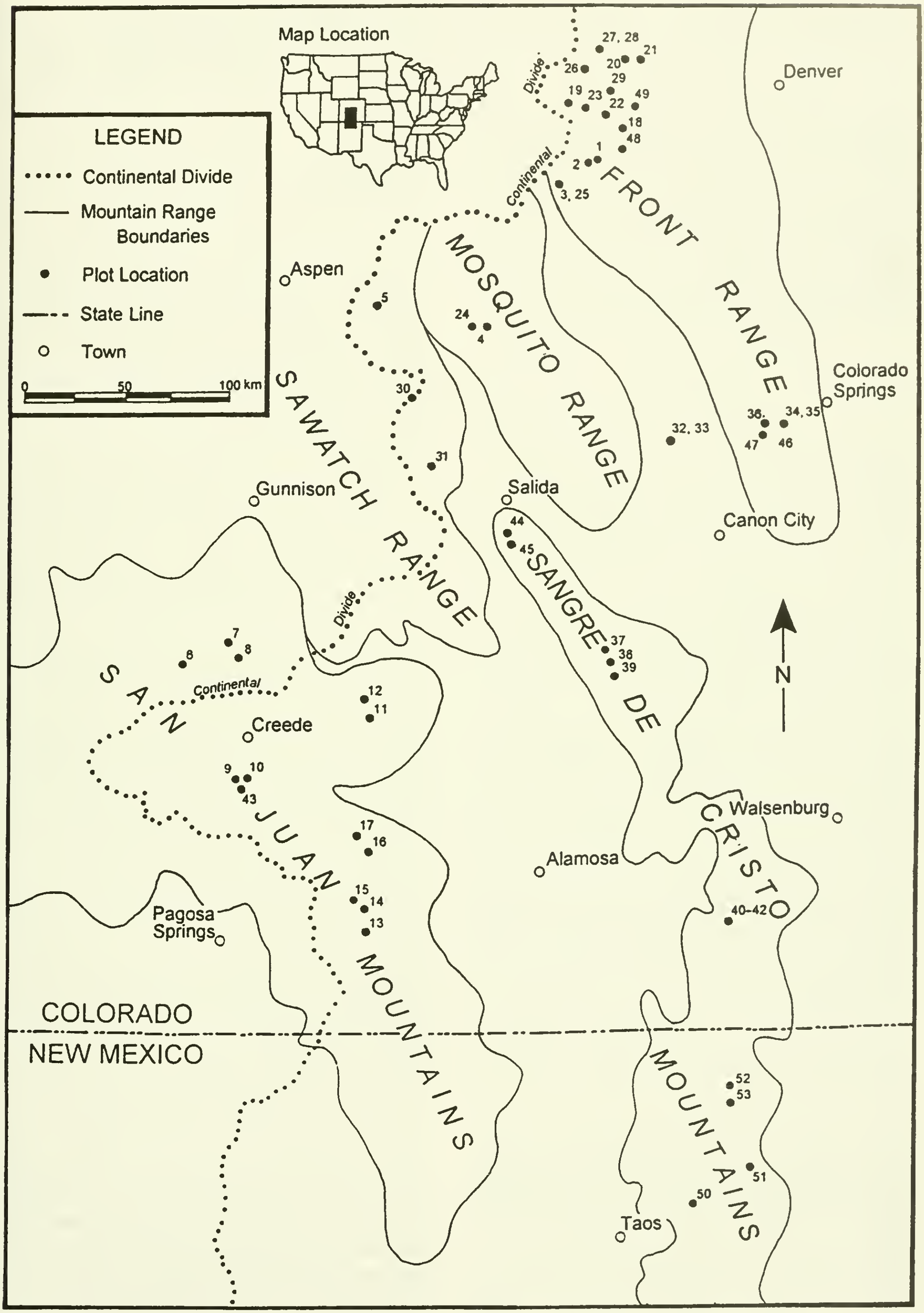
The geology of *P. aristata* forests, where they occur, varies greatly among mountain ranges. In the Front Range, *P. aristata* forests are found on Precambrian granites (Scott et al. 1984). Stands in the Mosquito Range may occur on Precambrian granites or Pennsylvanian sandstone (Tweto et al. 1978). Middle Tertiary intrusive rocks, Laramide intrusive rocks, Precambrian granite, or Felsic and Hornblendic gneisses underlie stands in the Sawatch Range (Tweto et al. 1978). In the San Juans, *P. aristata* forests grow on pre-ashflow andesitic lavas, breccias, tuffs, and conglomerates or ashflow tuff; in the Sangre de Cristos, stands are underlain by Pennsylvanian-Permian sandstones, siltstones, and conglomerates (Tweto et al. 1978, Tweto 1979).

Fire, snow avalanches, livestock grazing, logging, mining, and tourism are important disturbance agents in *P. aristata* forests. Fire, often started by lightning strikes, appears to encourage *P. aristata* regeneration (Baker 1992). Snow avalanches have removed large patches of *P. aristata* forests, resulting in alternating strips with and without forest. Cattle grazing occurs in the more accessible stands, and sheep grazing occurs at high elevations, especially in the San Juans. Early miners valued the dense wood of the bristlecone pine for shoring up mine shafts.

METHODS

Site Selection

Sampling sites were selected mainly from those previously located by Baker (1992). A site is a location bounded by the limits of its contiguous *P. aristata* forests. Additional sites were chosen from stands sampled by Brunstein and Yamaguchi (1992) and from areas recommended by the USDA Forest Service. To ensure that a wide range of variation in *P. aristata* forest vegetation was sampled, sites were selected to fill "cells" defined by a stratification of elevation and geography (Table 1). Elevation was divided into three 300-m-wide categories, ranging from 2750 to 3650 m. The range of *P. aristata* in Colorado was divided into 4 geographical units based on mountain ranges: the Front, San Juan, Sangre de Cristo, and Sawatch-Mosquito ranges. Only sites with low cover by exotic plant species, no recent evidence of livestock grazing, and no other signs of significant human alteration were selected. Sampled sites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Colorado Springs
Gunnison
Salida
Canon City
Creede
Walsenburg
Alamosa
Pagosa Springs
Taos
FRONT RANGE
MOSQUITO RANGE
SAWATCH RANGE
SANGRE DE CRISTO MOUNTAINS
SAN JUAN MOUNTAINS
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Donna Weatherman 1995

Fig. 1. Study area map. Numbers are plot numbers. The 4 plots in New Mexico were sampled by DeVelice et al. (1986).

were restricted to mature forests that originated prior to Euro-American settlement.

Vegetation Sampling

Forty-nine 0.1-ha (20 × 50-m) plots were sampled, with as many as 3 plots placed at different elevations in a single site. Each plot was placed in a representative location within the site. A visual estimation of percent canopy cover was made for every vascular plant species rooted in the plot after walking a transect completely traversing the plot. Estimates for plants with less than 10% cover were made in 1% increments, with 10–25% cover in 5% increments, and with greater than 25% cover in 10% increments. Plant nomenclature follows PLANTS, a standardized national list of plant names (USDA Natural Resource Conservation Service 1995). A voucher specimen of each species was deposited in the Rocky Mountain Herbarium in Laramie, Wyoming. Four plots from New Mexico, sampled by DeVelice et al. (1986), are also included in our analysis.

Tree age and size-class structure data were from Baker (1992) and Brunstein and Yamaguchi (1992). Where tree data were unavailable from a previous study, all living tree stems in a stand were tallied by species and size class. Woody stems <1 m tall were tallied as seedlings and small saplings. Stems >1 m tall with a diameter at breast height (dbh) of <2.5 cm were tallied as large saplings. The remaining tree size classes were in 5-cm-wide increments. Tree age was determined using cores extracted just above ground level from 5–15 of the largest trees. Due to imprecision in dating and the possibility of missing rings, tree ages were recorded in 25-yr classes.

Environmental and Geographic Data

Environmental and geographic variables recorded for each plot were chosen based on a literature review of the factors affecting vegetation structure and composition in Rocky Mountain forests. Latitude and longitude were obtained from topographic maps. Mountain range was recorded as Front Range, Sawatch-Mosquito Ranges, Sangre de Cristos, or San Juans. Elevation was measured with an altimeter, and slope and aspect were measured using a compass and clinometer. The topographic position of each plot was recorded as bottom (valley), lower 1/3 slope, middle 1/3 slope, top 1/3 slope, or ridgetop. Parent material was classified as intrusive igneous, extrusive igneous, sedimentary, or metamorphic. Within each plot percent rock cover was estimated as 0–25%, 26–50%, 51–75%, and 76–100%. Mean rock size at the soil surface was recorded as 0–1 m, 1–2 m, or >2 m. Litter depth was classified as <2 cm or >2 cm.

TABLE 1. Number of sites sampled in each cell. Cells are based on geographic and elevational divisions.

	2750 to 3050 m	3050 to 3350 m	3350 to 3670 m
Front Range	5	6	10
San Juans	3	9	1
Sangre de Cristos	2	6	4
Sawatch-Mosquitos	—	4	3

Soil was collected from the upper 15 cm of the profile every 5 m along the 50-m center line of the rectangular plot. Soil depth for the plot was an average based on the depth of soil above the C horizon at each of the 10 collection points. These 10 subsamples were mixed to form the plot sample, sieved to 2 mm, and dried at 100°C for 24 h prior to the analyses (pH, percent nitrogen, and percent organic carbon). Soil pH was measured on 7 g of soil 30 min after it had been mixed with 35 ml of 0.01 m $CaCl_2$. For the soil carbon and nitrogen analyses, the soil was ground to a fine powder in a ball mill, carbonates were liberated with acid, and 0.1-g samples were analyzed in a LECO CHN analyzer. Year-old foliage was collected from the south side of a *P. aristata* every 10 m along the 50-m plot center line. The foliage samples were air-dried for storage, then dried for 24 h at 70°C, ground to pass 40 mesh, and analyzed for nitrogen and phosphorus by autoanalysis of Kjeldahl digests (Anonymous 1992a, 1992b). Soil texture was determined by hand and recorded in general texture categories: loam, sandy loam, and loamy sand.

Gradient Analysis and Classification

The understory species composition data were ordinated with both indirect and direct gradient analysis using CANOCO (Canonical Community Ordination; ter Braak 1988). Ordination arranges species or plot samples along an axis based on their similarities. Soil chemical data were logarithmically transformed because with resource data, such as soil nutrients and rainfall, the difference between 1 and 10 is likely to be more significant to plants than the difference between 1000 and 1010 (Palmer 1993). Non-categorical environmental variables were checked for normality, and all were found, by visual inspection, to be approximately normally distributed.

Detrended correspondence analysis (DCA) is an indirect gradient analysis technique useful for revealing the major patterns of variation in plant community composition. In DCA, Pearson's correlation can be calculated between the axis scores and the environmental variables to assess how strongly the variable is related to the variation in community composition. Canonical correspondence analysis (CCA) is a direct ordination method to relate species composition data directly to environmental variables (Palmer 1993). Thus, CCA has the additional capacity to directly identify the important environmental gradients (ter Braak 1986). In CCA the correlation between an environmental variable and an ordination axis (intraset correlation) indicates the importance of that variable in defining the ordination axis (ter Braak 1986).

Comparison of DCA and CCA results reveals how much of the variation in the understory species data is explained by the measured environmental variables (ter Braak 1986). Eigenvalues measure the separation of species or plot distributions along the ordination axis (ter Braak 1988). An eigenvalue close to 1 indicates a high correspondence between plot scores and species scores, and eigenvalues near 0 represent low correspondence (Palmer 1993). If eigenvalues from DCA and CCA analyses are similar, one can assume that the measured environmental variables explain the main variation in species composition data (ter Braak 1986). Large differences between the 2 solutions suggest that an important environmental variable(s) was not measured. Species-environmental correlations are a measure of how well environmental variables explain the detected variation in community composition (ter Braak 1986).

Groups consisting of similar plots were identified using the SPSS/PC+ program for cluster analysis (Marija 1988). The cosine distance measure and the BAVERAGE method (average linkage between groups) were found to produce the most meaningful classification. Because cluster analysis of combined overstory and understory data often produces groups that reflect only the high cover values of the overstory species, understory and overstory data were clustered separately (Walford and Baker 1995). Results of the 2 analyses were then compared to determine if the overstory clusters correspond with the understory groups. Dendrograms from cluster analysis do not automatically produce a classification. To choose a single consistent level of similarity at which the groups are best defined, we worked down through the levels of the dendrogram until we found classification units that are internally homogenous (high constancy), compositionally distinct, and in a distinct environment.

RESULTS

Gradient analysis

Eigenvalues for the DCA and CCA analyses are similar (Table 2), suggesting that measured environmental variables explain most of the variation between plots (ter Braak 1986). Species-environment correlations are very high (Table 2), suggesting that the detected variation in species composition between plots is well explained by environmental variables. The strongest environmental and geographic correlates with plot composition are represented by arrows on the CCA ordination diagram (Fig. 2). The length of the arrow is a measure of the magnitude of differences in plot distribution along that environmental variable (ter Braak 1986).

Environmental and geographic variables with the highest Pearson (DCA) or intraset (CCA) correlation coefficients are those most strongly related to the variation in plot composition (Table 3). Elevation, soil pH, location in the San Juans, and extrusive igneous parent material correlate most strongly with the first DCA and CCA axis (Table 3). Values for pH were between 4.47 and 6.85. Weaker variables

TABLE 2. Eigenvalues and species-environment correlation coefficients for the detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA).

	Axis 1	Axis 2	Axis 3	Axis 4
		Eigenvalues		
DCA	0.675	0.385	0.263	0.215
CCA	0.645	0.363	0.351	0.278
		Species-environment correlation coefficients		
DCA	0.972	0.896	0.862	0.858
CCA	0.981	0.921	0.950	0.956

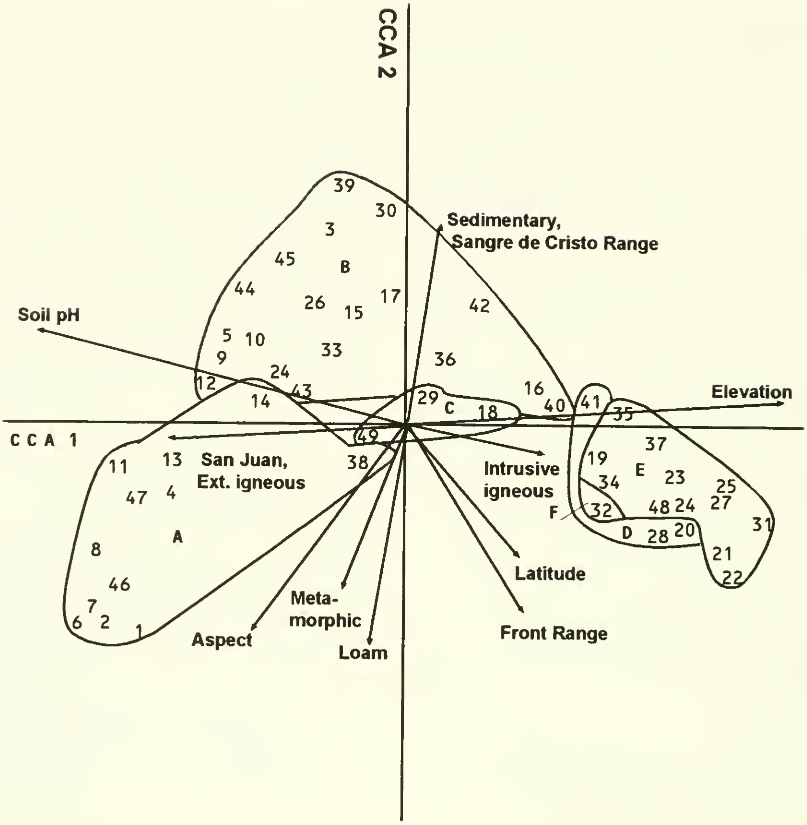


Fig. 2. Canonical correspondence analysis (CCA) ordination diagram. The most important environmental and geographic variables are illustrated by arrows. Letters represent plant associations identified in the classification: **A** = *Pinus aristata / Festuca arizonica*, **B** = *Pinus aristata / Festuca thurberi*, **C** = *Pinus aristata / Juniperus communis*, **D** = *Pinus aristata / Vaccinium myrtillus*, **E** = *Pinus aristata / Trifolium dasyphyllum*, **F** = *Pinus aristata / Ribes montigenum*. Numbers are plot numbers as illustrated in the study area map (Fig. 1).

on the first DCA and CCA axes include intrusive igneous parent material, location in the Front Range, longitude, latitude, plot age class, topographic position, and aspect (Table 3).

The second DCA axis scores are correlated with elevation and topographic position and weakly correlated with plot age, soil pH, and ratio of carbon to nitrogen (Table 3). The second CCA axis, however, had a moderate negative correlation with loamy soils, metamorphic parent material, aspect, and location in the Front Range, and a moderate positive correlation with sedimentary parent material and location in the Sangre de Cristos (Table 3).

As indicated by soil nitrogen and organic carbon and by foliar nitrogen, site fertility varied widely among bristlecone pine stands. For example, foliar nitrogen in 1-yr-old needles (an indicator of photosynthetic capacity) varied from 0.74% to 1.09%, and soil carbon-to-nitrogen ratio (an indicator of the availability of nitrogen for growth) varied from 10 to 33. Among sites, soil carbon-to-nitrogen ratio and foliar nitrogen were only weakly correlated (r = 0.41). Despite the wide variation in site fertility, soil and foliar nutrients were only weakly correlated with variation in plot composition.

Classification

The cluster analysis of the understory data suggested that the stands could be divided into 5 plant associations, 1 tentative plant association, and 3 outliers at the 20% similarity level. The 5 associations have distinct environmental settings, species composition, and species abundance. Group A, found in the lowest elevation *P. aristata* forests, is dominated by *Festuca arizonica. Festuca thurberi* dominates group B. Group C is characterized by an abundance of *Juniperus communis* and *Carex pityophila*

TABLE 3. Pearson's (DCA) and intraset (CCA) correlation coefficients of the first 2 axes with environmental and geographic variables. Coefficients ≥ 0.4 are in bold. Variables with all values <0.2 are not shown. Variables are listed in the order of their loadings.

	DCA		CCA	
Environmental variable	Axis 1	Axis 2	Axis 1	Axis 2
Elevation	**0.85**	**0.55**	**0.88**	0.07
Soil pH	**–0.72**	–0.33	**–0.75**	0.22
San Juan Range	**–0.46**	–0.15	**–0.47**	–0.00
Extrusive igneous	**–0.44**	–0.14	**–0.44**	–0.01
Intrusive igneous	0.39	0.21	**0.40**	–0.10
Longitude	–0.38	–0.12	–0.39	0.08
Latitude	0.36	0.12	0.37	–0.31
Topographic position	0.24	**0.47**	0.27	–0.27
Front Range	0.35	0.23	0.38	**–0.40**
Aspect	–0.27	0.04	–0.26	**–0.40**
Sedimentary	0.08	–0.10	0.07	**0.43**
Metamorphic	–0.12	–0.03	–0.11	**–0.41**
Loam	–0.08	–0.09	–0.08	**–0.43**
Sangre de Cristo Range	0.08	–0.10	0.07	**0.43**
Plot age class	0.29	0.38	0.31	–0.10
Soil carbon-to-nitrogen ratio	–0.05	–0.35	–0.08	–0.05
Percent rock cover	–0.04	0.28	–0.03	0.09
Mean rock size	0.15	0.22	0.16	0.07
Soil nitrogen	0.20	0.02	0.19	0.27
Foliar nitrogen	0.19	0.20	0.21	0.16
Soil organic carbon	0.16	–0.12	0.14	0.28
Foliar phosphorus	–0.04	–0.01	–0.04	–0.24

Mackenzie. *Vaccinium myrtilus* dominates group D, with *Juniperus communis* and *Carex foenea* Willd. present in all stands. The final group (E) is dominated by *Trifolium dasyphyllum.* A 6th plant association (F), dominated by *Ribes montigenum,* is tentatively identified based on plot 32 and previous research (DeVelice et al. 1986). A DCA ordination of the understory species data supports the 6 groups identified by cluster analysis (Fig. 3).

In addition, 2 phases were separated at a lower level of similarity. A *Ribes cereum* Dougl. phase (A1) of the *Pinus aristata / Festuca arizonica* association was identified, and a *Ribes cereum* phase (B1) can be separated from group B. Both phases, while sharing many common species with their respective associations, have a distinct set of species not common to the stands of the associations and occur in a slightly different environmental setting.

All associations are dominated by *P. aristata,* but the structure and composition of associated tree species vary (Fig. 4). A cluster analysis of the overstory data alone suggested that differences in overstory composition are insufficient to warrant splitting groups identified by clustering the understory data. The understory appears to be more sensitive than the overstory to environmental conditions.

Plant Associations

The environmental setting, tree species composition and structure, and understory species composition for each plant association and phase are described below. More detailed information for each association or phase is provided in the table of understory mean cover and constancy values (Table 4), and in the summary of tree species age-class data (Fig. 4). A complete list of species cover and constancy values, as well as summaries of the environmental variables determined to influence species composition, is given for each association and phase in Ranne (1995).

[A] *Pinus aristata / Festuca arizonica*

The overstory of this association, represented in 6 stands, is dominated by *P. aristata. Pinus flexilis* and *Populus tremuloides* Michx. are often present, and *Pinus ponderosa* P. & C. Lawson and *Pseudotsuga menziesii* (Mirbel) Franco are occasional associates. The shrub layer is sparse, with less than 10% cover. *Juniperus communis* is the most abundant shrub, with

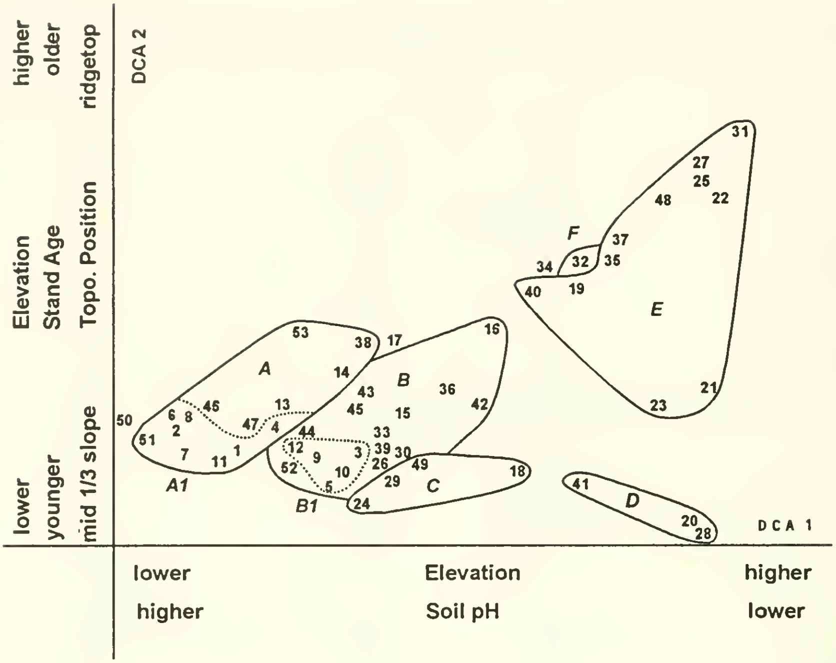


Fig. 3. Detrended correspondence analysis (DCA) ordination diagram. Environmental variables with the highest correlations with the axes are labeled along each axis. Letters represent plant associations identified in the classification: **A** = *Pinus aristata / Festuca arizonica*, **B** = *Pinus aristata / Festuca thurberi*, **C** = *Pinus aristata / Juniperus communis*, **D** = *Pinus aristata / Vaccinium myrtillus*, **E** = *Pinus aristata / Trifolium dasyphyllum*, **F** = *Pinus aristata / Ribes montigenum*. Dotted lines indicate phases: **A1** = *Pinus aristata / Festuca arizonica : Ribes cereum* phase, **B1** = *Pinus aristata / Festuca thurberi : Ribes cereum* phase. Numbers are plot numbers as illustrated in the study area map (Fig. 1).

Artemisia frigida Willd. and *Clematis columbiana* (Nutt.) Torr. & Gray occurring in small amounts. *Festuca arizonica* dominates the understory. Other common graminoids include *Koeleria macrantha* and *Carex foenea*. *Maianthemum stellatum* (L.) Link is the most common forb.

This association occurs in the lowest elevation *P. aristata* forests, between 2913 m and 3404 m. Stands were found in the Front, San Juan, Sangre de Cristo, and Mosquito ranges, on slopes ranging from 18% to 76%. A *Pinus aristata / Festuca arizonica* habitat type was described by Komarkova et al. (1988) in the San Juans and by DeVelice et al. (1986) in the Sangre de Cristos of New Mexico.

[A1] *Pinus aristata / Festuca arizonica : Ribes cereum* phase

The description of this phase is based on 8 stands. Composition of associated tree species is similar to that of group A. The understories of both the association and phase are dominated by *Festuca arizonica*. However, the phase is distinguished from association A by an abundance of *Ribes cereum*. Also distinctive is the abundance of *Carex pityophila*, high percent cover of *Muhlenbergia montana* (Nutt.) A.S. Hitchc. and *Koeleria macrantha*, and a set of forb species not present in association A. This phase occurs at similar elevations as the *Pinus aristata / Festuca arizonica* association, but on rockier slopes. It was identified in the Front, San Juan, and Mosquito ranges.

[B] *Pinus aristata / Festuca thurberi*

Pinus aristata is the dominant tree species. *Pinus flexilis*, when present, has a size-class structure similar to *Pinus aristata*, but it is much less abundant (Fig. 4). *Populus tremuloides* and/or *Picea engelmannii* Carr. is often present. The shrub layer is sparse, with *Juniperus communis* and *Rosa acicularis* Lindl. the most common species. The understory is dominated by *Festuca thurberi* in all 11 stands. *Koeleria macrantha*, *Carex foenea*, and *Achillea millefolium* DC. are usually present.

The elevation range for this association is between 3100 and 3600 m, usually above the *Pinus aristata / Festuca arizonica* association. The *P. aristata / Festuca thurberi* association

TABLE 4. Mean percent cover and constancy ( ) values for common (≥ 0.1% cover in at least 1 association) and constant (≥ 50% constancy in at least 1 association) species in the plant associations and phases, tr = <0.1%. A = *Pinus aristata / Festuca arizonica*, A1 = *Pinus aristata / Festuca arizonica : Ribes cereum* phase, B = *Pinus aristata / Festuca thurberi*, B1 = *Pinus aristata / Festuca thurberi : Ribes cereum* phase, C = *Pinus aristata / Juniperus communis*, D = *Pinus aristata / Vaccinium myrtilus*, E = *Pinus aristata / Trifolium dasyphyllum*, F = *Pinus aristata / Ribes montigenum*.

Association / Phase Number of Stands	A (6)	A1 (8)	B (11)	B1 (5)	C (4)	D (3)	E (12)	F (1)
SHRUBS								
Arctostaphylos uva-ursi (L.) Spreng.	.5 (33)	0 (0)	.5 (9)	2.4 (60)	1.8 (75)	.3 (13)	.2 (17)	0 (0)
Artemisia frigida Willd.	.7 (67)	1.7 (100)	.1 (18)	.2 (60)	0 (0)	0 (0)	0 (0)	0 (0)
Clematis columbiana (Nutt.) Torr. & Gray	.9 (67)	.1 (30)	tr (18)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Juniperus communis L.	1.7 (67)	2.3 (63)	3.6 (73)	6.4 (80)	9.0 (100)	6.0 (100)	.7 (45)	1.0 (100)
Pentaphylloides floribunda (Pursh) A. Love	.7 (67)	.4 (25)	.6 (27)	1.2 (60)	tr (25)	.3 (0)	.5 (43)	0 (0)
Ribes cereum Dougl.	0 (0)	7.4 (100)	.4 (27)	2.6 (100)	0 (0)	0 (0)	.4 (8)	0 (0)
Ribes montigenum McClatchie	.3 (17)	0 (0)	.2 (9)	0 (0)	tr (25)	.3 (33)	2.2 (57)	5.0 (100)
Rosa acicularis Lindl.	.7 (50)	.6 (50)	1.1 (67)	5.4 (60)	1.8 (75)	0 (0)	.3 (8)	0 (0)
Rubus idaeus L.	0 (0)	0 (0)	tr (9)	0 (0)	0 (0)	0 (0)	0 (0)	tr (100)
Vaccinium myrtillus L.	tr (17)	0 (0)	tr (9)	0 (0)	.8 (25)	25.0 (100)	1.0 (17)	0 (0)
GRASSES								
Bromus ciliatus L.	tr (33)	1.5 (25)	2.8 (73)	1.1 (80)	1.0 (25)	2.3 (33)	.5 (17)	0 (0)
Danthonia parryi Scribn.	1.0 (50)	tr (13)	.1 (9)	.4 (20)	0 (0)	0 (0)	0 (0)	0 (0)
Elymus elymoides (Raf.) Swezey	.2 (50)	tr (25)	tr (9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Elymus trachycaulus ssp. *trachycaulus* (Link) Gould ex Shinners	0 (0)	tr (25)	.5 (36)	0 (0)	0 (0)	0 (0)	.2 (25)	0 (0)
Festuca arizonica Vasey	13.8 (100)	18.0 (100)	1.3 (18)	2.0 (67)	tr (25)	0 (0)	.3 (17)	tr (100)
Festuca ovina L.	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3.0 (100)
Festuca thurberi Vasey	.7 (50)	tr (13)	13.1 (100)	18.0 (100)	0 (0)	2.7 (33)	.8 (25)	0 (0)
Koeleria macrantha (Ledeb.) J.A. Schultes	2.0 (83)	4.1 (88)	1.5 (73)	2.2 (80)	.5 (25)	0 (0)	.1 (25)	tr (100)
Muhlenbergia montana (Nutt.) A.S. Hitchc.	2.5 (50)	4.4 (75)	.4 (27)	2.6 (60)	0 (0)	0 (0)	0 (0)	0 (0)
Poa fendleriana (Steud.) Vasey	.1 (50)	1.5 (38)	.6 (18)	1.4 (80)	0 (0)	0 (0)	.4 (33)	0 (0)
Poa glauca ssp. *rupicola* (Nash ex Rydb.) W.A. Weber	0 (0)	.3 (13)	.2 (18)	0 (0)	0 (0)	0 (0)	.9 (50)	0 (0)
Poa interior Rydb.	.7 (33)	0 (0)	.4 (27)	0 (0)	0 (0)	0 (0)	.3 (17)	0 (0)
Poa leptocoma Trin.	0 (0)	0 (0)	.1 (18)	0 (0)	0 (0)	0 (0)	.7 (33)	2.0 (100)
Poa reflexa Vasey & Scribn. ex Vasey	.3 (17)	.3 (50)	.2 (27)	.6 (60)	1.0 (50)	0 (0)	.2 (17)	1.0 (100)
Trisetum spicatum (L.) Richter	.2 (17)	0 (0)	.7 (27)	.2 (20)	.5 (50)	.3 (33)	2.7 (83)	0 (0)

TABLE 4. Continued.

Association / Phase Number of Stands	A (6)	A1 (8)	B (11)	B1 (5)	C (4)	D (3)	E (12)	F (1)
SEDGES								
Carex foenea Willd.	2.8 (83)	.4 (13)	2.9 (73)	1.2 (40)	.3 (25)	5.3 (100)	8.8 (83)	0 (0)
Carex pityophila Mackenzie	tr (17)	2.9 (75)	.3 (9)	4.8 (100)	3.3 (100)	1.7 (33)	1.0 (33)	4.0 (100)
FORBS								
Achillea millefolium var. *occidentalis* DC.	.5 (67)	tr (25)	1.3 (91)	.6 (60)	tr (25)	1.7 (100)	1.3 (75)	0 (0)
Allium cernuum Roth	.4 (50)	tr (25)	.3 (27)	.2 (40)	0 (0)	0 (0)	0 (0)	tr (100)
Androsace septentrionalis L.	tr (17)	.2 (75)	tr (18)	tr (40)	0 (0)	0 (0)	tr (8)	0 (0)
Antennaria parvifolia Nutt.	.5 (75)	tr (38)	tr (18)	tr (40)	0 (0)	0 (0)	0 (0)	0 (0)
Antennaria rosea Greene	tr (17)	0 (0)	.7 (54)	tr (40)	0 (0)	.1 (100)	.6 (75)	0 (0)
Arabis drummondii Gray	.2 (17)	0 (0)	.1 (55)	.1 (60)	tr (25)	tr (33)	.1 (50)	0 (0)
Arabis fendleri (S. Wats.) Greene	.1 (50)	.2 (75)	0 (0)	.4 (60)	tr (25)	tr (33)	tr (8)	tr (100)
Arenaria fendleri Gray	.4 (50)	tr (25)	.4 (18)	0 (0)	0 (0)	.4 (13)	1.3 (83)	0 (0)
Artemisia ludoviciana Nutt.	.4 (33)	.7 (50)	tr (18)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Artemisia scopulorum Gray	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	.4 (50)	0 (0)
Campanula rotundifolia L.	tr (33)	.1 (25)	.8 (45)	1.0 (80)	.3 (25)	1.3 (67)	.5 (67)	0 (0)
Castilleja integra Gray	.2 (33)	tr (13)	.2 (18)	0 (0)	0 (0)	.4 (67)	.2 (42)	0 (0)
Descurainia incana ssp. *incana* (Bernh. ex Fisch. & C.A. Mey.) Dorn	0 (0)	tr (13)	0 (0)	.1 (60)	0 (0)	0 (0)	0 (0)	1.0 (100)
Draba aurea Vahl ex Hornem.	.1 (50)	.1 (25)	.1 (36)	.4 (80)	.1 (50)	0 (0)	.1 (50)	0 (0)
Epilobium angustifolium L.	tr (33)	0 (0)	.5 (36)	.4 (60)	tr (25)	.1 (67)	.4 (58)	0 (0)
Erigeron compositus Pursh	0 (0)	0 (0)	tr (9)	0 (0)	0 (0)	0 (0)	.3 (8)	2.0 (100)
Erigeron speciosus (Lindl.) DC.	.2 (17)	0 (0)	.3 (9)	1.2 (80)	0 (0)	0 (0)	0 (0)	0 (0)
Erigeron subtrinervis Rydb. ex Porter & Britt.	1.3 (50)	.4 (63)	1.4 (45)	tr (40)	tr (25)	0 (0)	.1 (8)	0 (0)
Fragaria vesca L.	0 (0)	tr (13)	tr (9)	.4 (60)	.3 (8)	0 (0)	.1 (8)	0 (0)
Frasera speciosa Dougl. ex Griseb	.2 (17)	0 (0)	0 (0)	0 (0)	.3 (50)	tr (33)	tr (8)	0 (0)
Geranium viscosissimum Fisch. & C.A. Mey. ex C.A. Mey.	0 (0)	.9 (63)	.2 (18)	0 (0)	tr (25)	0 (0)	0 (0)	0 (0)
Geum rossii var. *turbinatum* (Rydb.) C.L. Hitchc.	0 (0)	0 (0)	.1 (18)	0 (0)	0 (0)	.3 (33)	1.3 (58)	0 (0)

TABLE 4. Continued.

Association / Phase Number of Stands	A (6)	A1 (8)	B (11)	B1 (5)	C (4)	D (3)	E (12)	F (1)
FORBS (continued)								
Heterotheca villosa (Pursh) Shinners	.3 (17)	tr (13)	.6 (27)	0 (0)	.1 (50)	tr (33)	.5 (50)	0 (0)
Heuchera bracteata (Torr.) Ser.	0 (0)	.1 (13)	.1 (18)	0 (0)	.1 (50)	tr (33)	.1 (50)	0 (0)
Maianthemum stellatum (L.) Link	.7 (83)	.3 (25)	.6 (54)	1.4 (100)	.5 (25)	0 (0)	0 (0)	0 (0)
Mertensia lanceolata (Pursh) DC.	0 (0)	.5 (75)	.2 (27)	.4 (60)	0 (0)	0 (0)	.4 (50)	0 (0)
Minuartia obtusiloba (Rydb.) House	.2 (17)	0 (0)	.5 (27)	0 (0)	.3 (25)	0 (0)	1.0 (83)	2.0 (100)
Penstemon whippleanus Gray	0 (0)	0 (0)	.1 (27)	0 (0)	5 (50)	.4 (100)	.4 (67)	0 (0)
Polemonium pulcherrimum ssp. *delicatum* (Rydb.) Brand	tr (17)	0 (0)	tr (9)	0 (0)	0 (0)	.1 (67)	.6 (58)	0 (0)
Potentilla fissa Nutt.	.7 (33)	.6 (25)	.3 (36)	0 (0)	.1 (50)	0 (0)	0 (0)	0 (0)
Potentilla pensylvanica L.	0 (0)	0 (0)	0 (0)	tr (20)	0 (0)	0 (0)	0 (0)	tr (100)
Potentilla rubricaulis Lehm.	.7 (33)	.1 (25)	.1 (9)	.6 (60)	0 (0)	0 (0)	.2 (25)	0 (0)
Pseudocymopterus montanus (Gray) Coult. & Rose	.1 (50)	tr (13)	.7 (54)	.7 (80)	tr (25)	0 (0)	0 (0)	0 (0)
Sedum stenopetalum Pursh	.7 (50)	.4 (38)	.1 (36)	.2 (20)	.1 (50)	.1 (67)	.7 (92)	0 (0)
Senecio fendleri Gray	.5 (50)	.2 (8)	.7 (45)	.6 (60)	.8 (50)	.7 (33)	.5 (33)	2.0 (100)
Senecio pudicus Greene	tr (17)	tr (13)	tr (9)	.8 (60)	0 (0)	0 (0)	0 (0)	0 (0)
Solidago simplex ssp. *simplex* var. *nana* (Gray) Ringius	.7 (50)	0 (0)	.6 (36)	0 (0)	.3 (25)	2.0 (100)	1.0 (75)	0 (0)
Thermopsis rhombifolia var. *divaricarpa* (A. Nels.) Isely	.5 (33)	0 (0)	2.7 (60)	tr (20)	0 (0)	0 (0)	0 (0)	0 (0)
Trifolium dasyphyllum Torr. & Gray	.5 (17)	0 (0)	1.4 (40)	0 (0)	1.5 (25)	6.3 (100)	10.1 (100)	0 (0)
Woodsia oregana D.C. Eat.	tr (33)	tr (13)	tr (20)	.1 (60)	0 (0)	tr (33)	0 (0)	0 (0)
Zigadenus elegans Pursh	0 (0)	0 (0)	.1 (60)	0 (0)	tr (25)	tr (33)	tr (8)	0 (0)

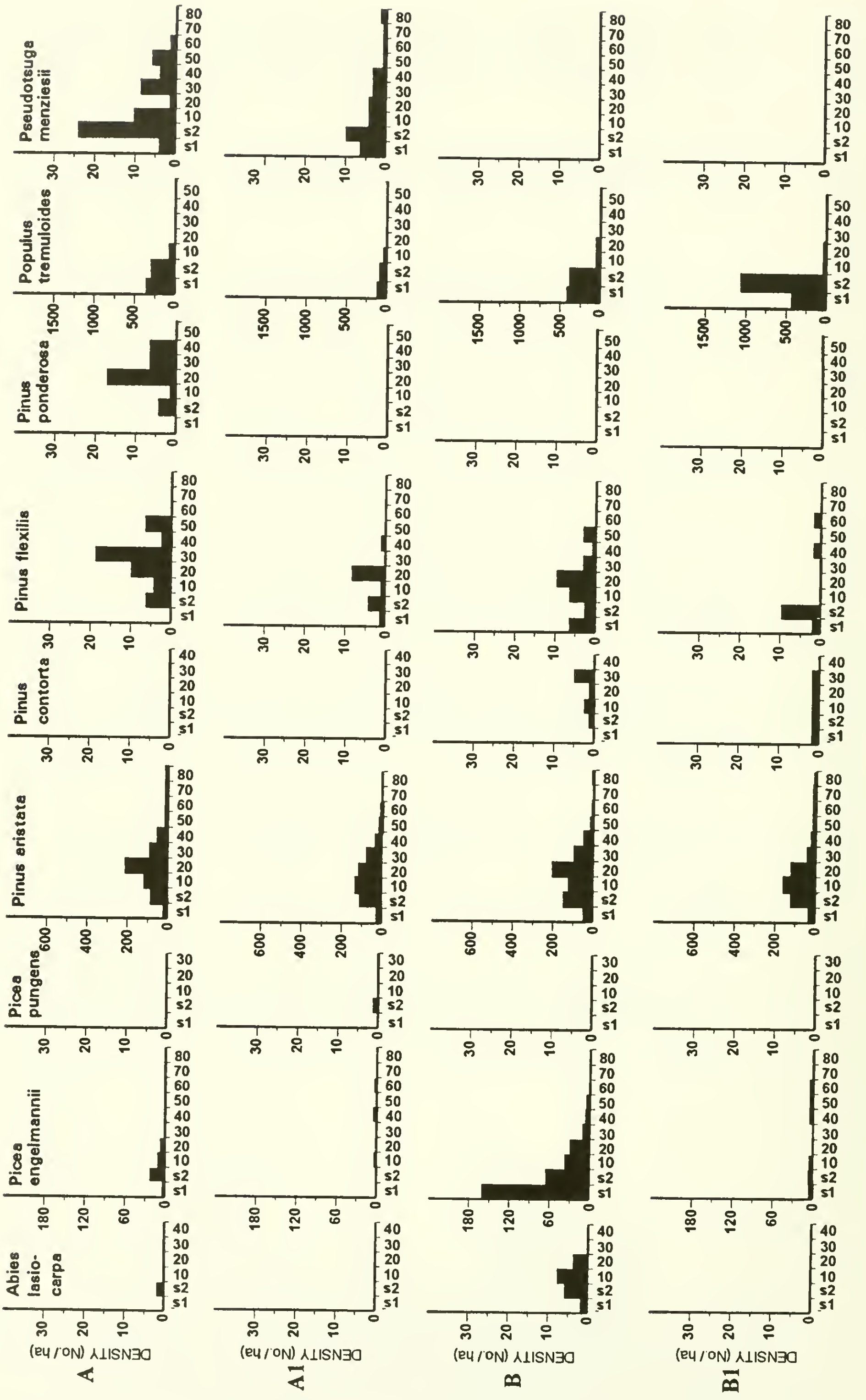
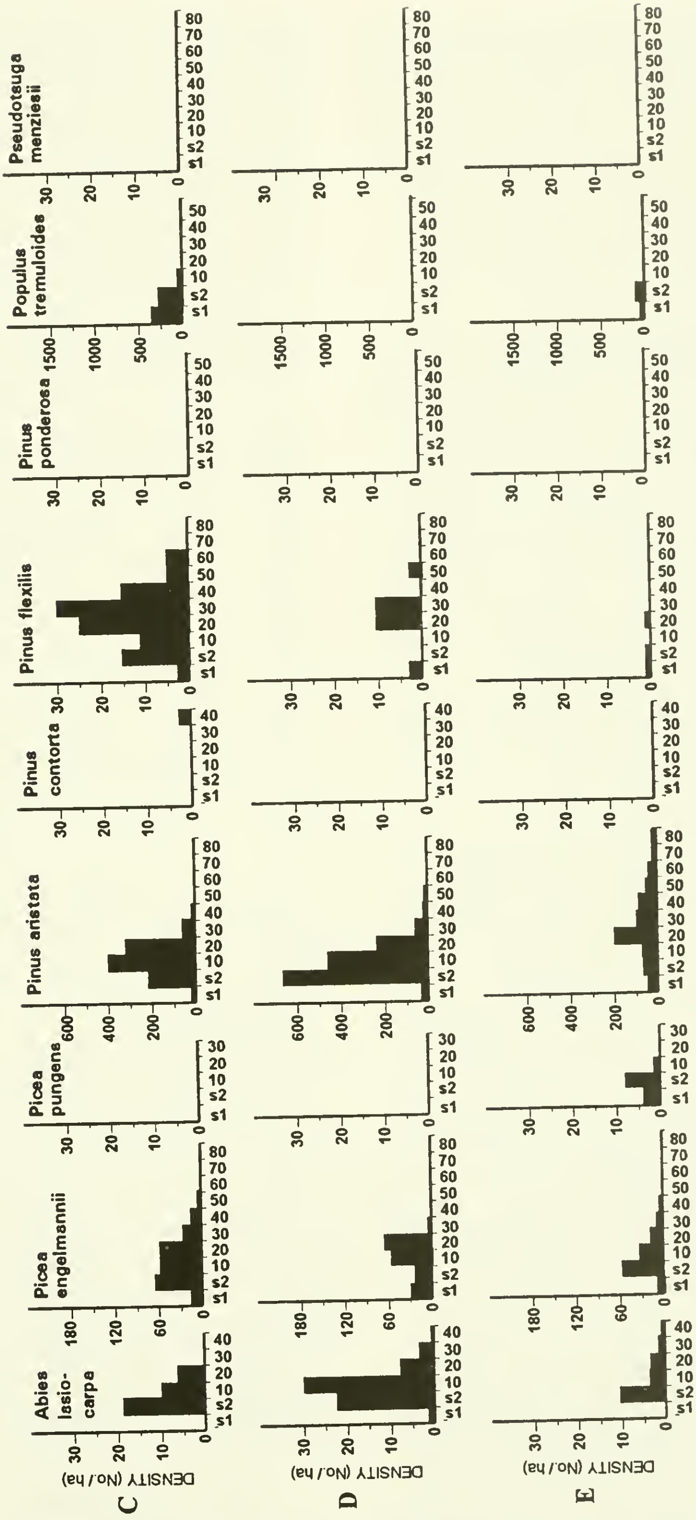


Fig. 4. Mean overstory stem density (number of stems per ha) by species, within plant associations and phases. Note that the vertical axes vary with the species. A = *Pinus aristata / Festuca arizonica*, A1 = *Pinus aristata / Festuca arizonica : Ribes cereum* phase, B = *Pinus aristata / Festuca thurberi*, B1 = *Pinus aristata / Festuca thurberi : Ribes cereum* phase,



C = *Pinus aristata / Juniperus communis*, D = *Pinus aristata / Vaccinium myrtillus*, E = *Pinus aristata / Trifolium dasyphyllum*, F = *Pinus aristata / Ribes montigenum*. Horizontal axes are tree size classes: s1 = seedlings and small saplings (stems <1 m tall), s2 = large saplings (stems >1 m tall, with a dbh <2.5 cm, remaining tree size classes are in 10-cm-wide increments (e.g., "10" means 10–20 cm) based on dbh.

was found in the Front Range, San Juans, and Sangre de Cristos. Komarkova et al. (1988) described a *Pinus aristata / Festuca thurberi* habitat type with similar species composition and environmental settings from 1 stand in the San Juans. DeVelice et al. (1986) also recognized a *Pinus aristata / Festuca thurberi* habitat type in the Sangre de Cristos and the San Juans.

[B1] *Pinus aristata / Festuca thurberi : Ribes cereum* phase

Overstory species composition is similar to group B. The shrub cover of this phase is much greater than in the previous association, with *Ribes cereum* present in all stands. *Juniperus communis* is usually present. *Festuca thurberi* dominates the understory, with *Bromus ciliatus* L., *Poa fendleriana*, and *Koeleria macrantha* occurring in most stands. *Carex pityophila* is present in all 5 stands. *Campanula rotundifolia* L., *Draba aurea* Vahl. ex Hornem., *Erigeron speciosus* (Lindl.) DC., and *Pseudocymopterus montanus* (Gray) Coult. & Rose are common forbs. This phase occurs at lower elevations than association B, between 2900 and 3100 m. It was found in the Front, San Juan, and Mosquito ranges.

[C] *Pinus aristata / Juniperus communis*

Pinus aristata dominates the overstory, and *Picea engelmannii* is an overstory associate. *Pinus flexilis* occurs in all but 1 stand. *Juniperus communis* has high cover values in all stands, and *Arctostaphylos uva-ursi* (L.) Spreng. and *Rosa acicularis* are often present. *Carex pityophila* is the only common, and the most abundant, graminoid. Grasses and herbaceous plants are sparse. This association was found only on intrusive igneous parent material (in the Front and Mosquito ranges) at elevations between 3233 and 3312 m. Komarkova et al. (1988) described a similar habitat type from a stand in the San Juans. Until now, this association was not described elsewhere in Colorado.

[D] *Pinus aristata / Vaccinium myrtilus*

Abies lasiocarpa (Hook.) Nutt., *Picea engelmannii*, and *Pinus flexilis* are associated tree species. *Vaccinum myrtilus* dominates the shrub layer in all 3 stands, and *Juniperus communis* is always present. *Carex foenea* is the only abundant and common graminoid. *Achillea millifollium, Antennaria rosea* Greene, *Penstemon whippleanus* Gray, *Solidago simplex* (Gray) Ringius, and *Trifolium dasyphyllum* occur in every stand. This association always occurs on the upper 1/3 of the slope, at elevations between 3343 and 3526 m, often near treeline. Stands of this association are underlain by intrusive igneous parent material and were found in both the Front and Sangre de Cristo ranges. Soil pH values (<5.1) are the lowest for any *P. aristata* association. This association has not been previously described.

[E] *Pinus aristata / Trifolium dasyphyllum*

Picea engelmannii is often present in the 12 stands of this association. The shrub layer is sparse, with the most common shrub, *Ribes montigenum*, occurring in only 57% of the stands. *Carex foenea* is the most prevalent and abundant graminoid. The understory is dominated by *Trifolium dasyphyllum. Sedum stenopetalum* Pursh and *Mertensia lanceolata* (Pursh) DC. are common forbs. This association occurs on the border of forest and alpine vegetation or on the ridgetops of lower peaks. Elevation range is between 3233 and 3633 m. It was located in the Front, Sawatch, Mosquito, and Sangre de Cristo ranges. A *Pinus aristata / Trifolium dasyphyllum* habitat type was reported by Hess and Alexander (1986) in the Front Range.

[F] *Pinus aristata / Ribes montigenum*

This plant association is tentatively described based on 1 stand (plot 32). The understory is dominated by *Ribes montigenum. Festuca ovina* L. and *Carex pityophila* are the most abundant graminoids. Abundant forbs include *Senecio fendleri* Gray, *Minuartia obtusiloba* (Rydb.) House, and *Erigeron compositus* Pursh. This association was found at an elevation of 3367 m on a scree slope. DeVelice et al. (1986) identified this habitat type also based on a single stand on a scree slope in the San Juans, but 5 of the most important species in the DeVelice et al. (1986) stand are missing from plot 32. Moreover, our single stand has many species in common with our *Pinus aristata / Trifolium dasyphyllum* association. Because of these discrepancies and the small number of known *Ribes montigenum*–dominated stands, this association is tentative.

DISCUSSION

Gradient Analysis

Elevation, which is a composite of environmental factors, was identified by both indirect and direct gradient analysis to be the most important variable influencing species composition. This is not surprising, as elevation has frequently been identified as the dominant variable influencing mountain vegetation (Ramaley 1907, Daubenmire 1943, Weber 1965, Whittaker 1967, Peet 1981, 1988, Allen and Peet 1990, Allen et al. 1991). With increasing elevation temperature decreases, and precipitation, snow depth, wind, and solar radiation increase (Peet 1988, Barry 1992). Allen and Peet (1990) found that increasing elevation was associated with decreasing pH, a relationship also identified in this study.

Soil pH values in *P. aristata* forests in this study (4.47–6.85) are slightly more acidic than previously reported pH values (5.6–7.7; Hess and Alexander 1986, Komarkova et al. 1988). Soil pH decreased with elevation, perhaps because high-elevation *P. aristata* forests are often underlain by granite, a parent material low in basic cations. Soil pH appears to directly influence community composition. For example, the 3 stands in the *Pinus aristata / Vaccinium myrtilus* association have low pH (<5.1); plants of the Ericaceae family, such as *Vaccinium myrtilus*, appear to grow better in highly acidic soils (Rendig and Taylor 1989).

Variation in geographic location and geologic substrate also influences composition in *P. aristata* forests. Geographic location involves a complex array of environmental factors, such as climate and isolation. Because geology varies with mountain ranges, these 2 variables are related. For example, the *P. aristata* stands in the Front Range grow primarily on intrusive igneous rock, while stands in the San Juans are found mainly on extrusive igneous rock. The type of parent material influences the chemistry and texture of the soil (Birkland 1984). Soils on extrusive igneous or sedimentary parent materials were, in general, finer textured than soils on intrusive igneous or metamorphic parent materials. Soils underlain by granite often had lower percent nitrogen and percent organic carbon than soils on other substrata. However, the relationship between parent material and nutrients was less distinct than the relationship between parent material and texture. The vegetation and distribution of Great Basin bristlecone pine (*Pinus longaeva*) forests in the White Mountains of California are also influenced by substrate (Mooney et al. 1962). *Pinus longaeva* are found at higher elevations on dolomite rather than on granite or sandstone, and granite supports a greater density of understory vegetation in these forests than does either dolomite or sandstone (Mooney et al 1962). Despain (1973) found that major forest vegetation types in the Big Horn Mountains are found on different geologic substrata.

Nutrient levels in the soils of *P. aristata* forests have not been studied prior to this research. Interestingly, we could not show soil fertility effects on plant species composition in *P. aristata* forests, even though many studies document the effect of fertility on productivity in forests in general.

Soil texture, which influences moisture availability, explained a moderate portion of the variation in community composition on CCA axis 2. More water is held in a form available to plants in finer soils than in coarser soils, but fine soils need more water to bring the water potential up to the range of availability of plants (Despain 1973). After a thunderstorm, coarse soils may therefore have more water available to plants (Despain 1973). Mooney et al. (1962) found that *Pinus longaeva* forests in the White Mountains vary along a soil moisture gradient related to substrate. The primary distinction in the *P. aristata* ordination is between loams and sandy loams. The finer, low-elevation loams may have less available water than the coarser, high-elevation soils.

The influence of aspect and topographic position on the ordination axes also suggests that soil moisture may be a factor influencing community composition. Calculations of soil moisture often incorporate indices of topographic position, potential solar radiation, and exposure (Birkland 1984, Allen and Peet 1990, Allen et al. 1991). Allen and Peet (1990) found that site moisture status was a major environmental factor controlling species composition in the Sangre de Cristos. Gradient analysis of 3 sites in the southern Rocky Mountains also revealed that soil moisture was related to a major compositional gradient (Allen et al. 1991).

Although not as influential as geographical location and substrate, variation in latitude and longitude did explain a small amount of the variation in plant community composition. Plots spanned a latitudinal range of approximately 3 degrees and a longitudinal range of approximately 2 degrees. Increases in latitude are associated with important climatic changes, such as larger annual temperature ranges

(Scott 1989). Peet (1978) found that composition of vegetation types changes with latitude in the southern Rocky Mountains. Yet, Allen et al. (1991) found that high-elevation *Picea engelmannii / Abies lasiocarpa* forests in the Rocky Mountains remained floristically similar over a smaller latitudinal range of 4 degrees. However, his plots were located at similar degrees of longitude in the easternmost ranges (Front and Sangre de Cristo) of the southern Rocky Mountains. Climatic differences between the eastern and western *P. aristata* stands may explain some of the variation. For example, maps of average annual precipitation indicate that some *P. aristata* stands near Pikes Peak may receive as little as 41 cm of precipitation per year, while other stands further west in the Sawatch and San Juan ranges receive between 102 and 152 cm (Krebs 1972, Brunstein and Yamaguchi 1992).

Classification

Prior to this research, knowledge of the distribution and composition of these associations was limited, due to small sample sizes and limited geographical sampling. A habitat type similar to the *Pinus aristata / Trifolium dasyphyllum* plant association had been recorded previously only in the Front Range (DeVelice et al. 1986). In this study we located this plant association in the Front, Sawatch, Mosquito, and Sangre de Cristo ranges. Similarly, Komarkova et al. (1988) described a *Pinus aristata / Juniperus communis* habitat from a single stand in the San Juans. Stands with the *Pinus aristata / Juniperus communis* plant association were described in this study in the Front and Mosquito ranges. Habitat types similar to the *Pinus aristata / Festuca arizonica* and *Pinus aristata / Festuca thurberi* plant associations had been described only in the San Juans and Sangre de Cristos (DeVelice et al. 1986, Komarkova et al. 1988). However, both were additionally located in the Front Range, and the *Pinus aristata / Festuca arizonica* association was also found in the Mosquito Range.

Previous researchers did not identify the phases of the *Pinus aristata / Festuca arizonica* and *Pinus aristata / Festuca thurberi* plant associations. It is important that these phases be recognized because of the differences between the shrub layers of the phases and their related plant associations. *Ribes cereum* is a dominant plant in the phases but is absent from the main plant associations. Differences in environmental settings and species composition between the phases and associations further illustrate the need to recognize these variations within the plant associations.

Of the 4 plots from New Mexico (DeVelice et al. 1986), 2 were included in the *Pinus aristata / Festuca arizonica* plant association, and 1 was included in the *Pinus aristata / Festuca thurberi* association. *Pinus aristata* stands in New Mexico are, in general, floristically similar to those in Colorado. However, an outlier, plot 50, may be representative of an association unique to New Mexico. Because only 4 plots from New Mexico were included in this analysis, a more thorough study of *P. aristata* stands in New Mexico is needed.

Classification provides a means of dividing the natural continuum of vegetation into distinct units useful for research, management, and conservation. The 6 plant associations identified in this study can be used as the foundation for selecting future Research Natural Area (RNA) sites. To insure that the range of natural variability of *P. aristata* forests is represented in the RNA system, sites should be selected to represent each plant association.

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DISPERSAL CHARACTERISTICS OF THE YUCCA WEEVIL (*SCYPHOPHORUS YUCCAE*) IN A FLOWERING FIELD OF *YUCCA WHIPPLEI*

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ABSTRACT.—Dispersal characteristics were measured for a population of yucca weevils (*Scyphophorus yuccae*) in a plot consisting of flowering and nonflowering *Yucca whipplei*. We compared weevil dispersal to yucca distribution, phenology, and caudex temperature. We also compared weevil movement to wind patterns and time of day. Captured weevils were marked and released into both flowering and nonflowering home plants in the field. Distance traveled, weevil flight direction, and target plant characteristics were recorded. We found that yucca weevils moved only between 1600 h on the release day and 0600 h of the following day. We recorded movement from both nonflowering and old flowering (>1/2 stalk had reached anthesis) yuccas to new flowering (>1/2 stalk pre-anthesis) yuccas. The pattern of weevil movement did not match the pattern of flowering yuccas in the field. Yucca weevils moved a mean distance of 33 ± 8 m. Caudex temperature appeared to be important for maintaining a population of weevils on a plant. Wind direction was the best predictor of weevil dispersal direction. Weevils consistently moved into the wind, suggesting that they are active fliers. Dispersal characteristics of the yucca weevil have implications for the evolution of the semelparous flowering strategy of *Y. whipplei* and *S. yuccae* life history.

Key words: Yucca whipplei, Scyphophorus yuccae, *yucca weevils, insect dispersal.*

Only 2 species in the genus *Scyphophorus* are known to exist in the New World (Vaurie 1971). *Scyphophorus acupunctatus* Gyllenhae and *Scyphophorus yuccae* Horn. (Curculionidae: Rhynchophorinae) are found exclusively on either agaves or yuccas, respectively (Vaurie 1971). The organism we studied was *S. yuccae*, the monophagous yucca weevil, which feeds on *Yucca whipplei* Torr. and other members of the genus *Yucca* in the southwestern region of the United States and Baja California (Waring 1986). The yucca weevil is a fully winged, flattened black beetle without scales or dorsal hairs, usually 10–19 mm long (Vaurie 1971). There is some evidence that *S. yuccae* damages the inflorescence of *Y. whipplei* in such a way that it influences the reproductive strategy of the plant (Huxman and Loik 1996). Therefore, dispersal characteristics of this weevil may be important in better understanding its influence on plant reproduction.

Yucca whipplei Torr. ssp. *whipplei* is a monocarpic perennial distributed throughout southern California, from the San Diego coast east and north into the Mojave Desert (Haines 1941, Aker 1982a). Each rosette has a several-year vegetative cycle and then produces a single large inflorescence. The inflorescence may produce between several hundred and several thousand flowers (Haines 1941), which can result in up to 150 fruit (Aker 1982b) and more than 15,000 seeds (Huxman 1996). The flowering season for the population of *Y. whipplei* in the San Gabriel Mountains (San Bernardino County, California) is typically from April through June, with individual plants in flower for a period that lasts between 2 and 7 wk (Aker 1982a). The inflorescence often develops for about 2 wk, reaching a height of 2 m before any flowers open, and extending to a final height of approximately 4 m.

Adult weevils usually occupy a low position on the plant (on both flowering and nonflowering rosettes); however, they feed and reproduce on the base of the flowering stalk (Coquillett 1892). During the summer and fall, *S. yuccae* larvae bore into the caudex and inflorescence of the yucca (Blaisdell 1892). They then travel up the inflorescence, making a network of tunnels and eventually reaching a position high in the stalk where they pupate and exit the plant, often before the plant drops seeds in September (Huxman and Loik 1996). Damage to the yucca inflorescence caused by tunneling weevils makes the plant more susceptible to wildfire damage (Huxman and Loik 1996). Fire damage

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and weevil tunnels can subsequently lead to the greater loss of small seed crops as compared to large seed crops in *Y. whipplei* (Huxman and Loik 1996).

In this study we test the hypothesis that *S. yuccae* actively disperses in a nonrandom pattern within a flowering field of *Y. whipplei.* We speculate that *S. yuccae* disperse in a directional-oriented pattern that is related to factors such as yucca phenology, wind patterns, or yucca caudex temperature. Because weevils damage small yucca inflorescences at a greater rate than large inflorescences (Huxman and Loik 1996), the dispersal characteristics of *S. yuccae* may be important in selecting for a large reproductive output and in the general evolution of semelparity in *Y. whipplei.*

METHODS

Study Site

The experimental plot is located within the San Bernardino National Forest in Day Canyon Wash (34°11′N, 117°32′W, 893 m). The plot is on alluvium, bisected by a permanent stream. Surrounding vegetation consists of a riversidian sagebrush scrub and chaparral mix composed of *Salvia apiana* Jeps., *Salvia mellifera* Greene, *Eriogonum fasciculatum* Benth., *Adenostoma fasciculatum* Eastw., *Quercus dumosa* Nutt., and *Ceanothus* spp. The plot is bordered to the north and west by the foothills of the San Gabriel Mountains; no geographic boundaries exist to the south or east. All experiments were carried out approximately 1 km from the base of the mountains to maintain a large homogeneous plot with respect to topography. Yearly rainfall estimates for Day Canyon Wash are 40–110 cm of precipitation, all as rain. During the 1994 experimental period, temperature for winter ranged from 4° to 15°C, while summer temperatures ranged from 17° to 34°C.

Experimental Design

During May and June 1990 and 1994, yucca weevils were randomly removed from rosettes adjacent to the experimental plot. Early in the flowering season, weevils were taken from nonflowering plants, but later they could be found only on flowering plants. Five to 10 weevils were taken from each plant. Once captured, they were kept in a container for no longer than 5 min, as extended periods of time could cause incidental flight upon release. Each weevil was subsequently marked on the pronotum with a small dot of Testor's (Testor Corporation, Rockford, IL) brand acetate paint and released into 1 of 2 field experiments.

In the 1st experiment we marked and released weevils into 8 randomly chosen home plants: 6 nonflowering and 2 flowering rosettes. Between 4 and 8 marked weevils were placed in each plant. Each individual home plant and its introduced weevils were marked with the same paint color, but different colors were used for different plant and weevil combinations. Weevils were released in the morning before 0800 h. In the afternoon of the release day (between 1600 h and 1800 h) we sampled the plots to look for any dispersed weevils. All *Y. whipplei* within the plot were sampled, and we repeatedly covered more than 3×10^4 m^2 during each sampling event. This represented the area within a 100-m radius from the release point of any weevil. In the morning (0600 h) and afternoon (1600 h) of the day following release, all *Y. whipplei* were sampled again. We measured the distance dispersed weevils had traveled from their specific home plant and noted the time of day as either morning or afternoon. In addition, plants on which dispersed marked weevils were found during sampling were categorized as either nonflowering, young flowering (>1/2 of flowers on stalk were pre-anthesis), or old flowering (>1/2 flowers on stalk had reached anthesis). This process was repeated 5 times within a 5-wk period from May through June 1990 and once in 1994.

In 1994 we mapped every *Y. whipplei* within a 100-m radius of a single home plant. The 100-m radius was greater than the maximum distance recorded for weevil dispersal in the 1990 field season. This mapped portion of the field was used for a 2nd experiment. Marked weevils were released in the morning (before 0800 h) into the single home plant. Plots were then sampled in the afternoon and morning of the following day to look for dispersed weevils in yuccas. We repeated this routine 5 times within a 3-wk period during May and June 1994, using the same home plant each time. During each release we marked the weevils with a different color paint. We released 28, 11, 20, 20, and 21 weevils, respectively, on 5 separate occasions and measured distance and direction weevils dispersed from the home plant. *Yuccas* on which marked weevils were found were categorized as either nonflowering, young flowering, or old flowering. Wind direction, determined from a hand-held piece of flagging, was assigned to 1 of 8 different 45° categories. Shade ambient temperature was measured for the morning and afternoon sampling periods with a copper-constantine thermocouple.

In a 3rd experiment in 1995, we recorded the temperature of the caudex (basal portion of the stem) of 20 mapped flowering *Y. whipplei* within a plot by inserting a copper-constantine thermocouple probe (Omega Company, Stamford, CT) approximately 1 cm into the caudex. The caudex temperature, which was recorded after the probe held a constant reading for more than 15 sec, was taken to be the mean of the temperatures of the north-, south-, east-, and west-facing sides of the caudex. We also censused the total number of weevils for each mapped flowering plant. Measuring caudex temperatures and censusing each mapped plant occurred at 0800, 1200, and 1800 h over 3 d in a week in June 1995. The 3 sampling events at each specific time were combined for each plant to produce a mean temperature and mean number of weevils present for each rosette at each time of day.

Statistical Analysis

We determined the mean angle of weevil dispersal from the home plant in the mapped field by back-calculating from the empirical mean vector of individual sampled weevil dispersal angles (Batschelet 1981). We tested dispersal patterns of weevils and the distribution of flowering *Y. whipplei* surrounding the home plant for randomness by the Rayleigh test. The pattern of weevil dispersal was compared to the pattern of flowering *Y. whipplei* by a χ^2 test (Batschelet 1981), and the weevil dispersal pattern with the sampled wind pattern for afternoon samples by a χ^2 test. To perform the latter test, weevil dispersal angles were placed into 45° categories to conform with wind data. Linear regression was used to compare the mean caudex temperature of flowering *Yuccas* to mean weevil population numbers on those *Yuccas* at each time of day. All data are expressed as mean ± 1 standard deviation.

RESULTS

The mean shade ambient temperature over the duration of this study was 18.1 ± 1.1°C (range 16–22°C) in the morning and 28.1 ± 1.3°C (range 26–33°C) in the afternoon.

During the first 2 experiments, 280 weevils were marked and released, 200 in the 1st experiment (1990 and 1994) and 80 in the 2nd (1994). In both experiments combined, 106 weevils were recaptured from plants other than their home plants (recovery rate 38%). In the 1st experiment 80 weevils were recovered (40%), and in the 2nd experiment 26 weevils were recovered (33%). When released into home plants, weevils moved to the center of the *Yucca* and maneuvered down close between the caudex and newly unfolded leaves.

All yucca weevils placed in nonflowering home plants moved to flowering *Y. whipplei* (Table 1). The mean distance weevils dispersed in the first experiment was 33 ± 8 m ($n = 75$). Some yucca weevils that were deposited in old flowering home plants moved 15 ± 2.5 m to new flowering *Yuccas* ($n = 4$), while others did not move at all, remaining in the flowering home plant ($n = 5$); however, the sample size for weevils initially released into old flowering *Yuccas* was quite small (Table 1). There was a significant difference between the distance weevils dispersed from nonflowering home plants and from flowering home plants (t test, df = 77, $P < 0.05$). The density of *Y. whipplei* within the field was 1.4×10^{-2} plants m^{-2}, with approximately 15% of the population flowering with a density of 2×10^{-3} plants m^{-2}.

In the 2nd experiment all weevils dispersed from the nonflowering home plant to flowering *Y. whipplei* (Table 1). Mean weevil dispersal distance was 18 ± 11 m ($n = 26$) from the home plant. The mean nearest-neighbor distance of flowering *Yuccas* was 11.63 ± 1.4 m. There was a significant difference between weevil dispersal distance and the mean nearest-neighbor distance of flowering *Y. whipplei* (t test, df = 125, $P < 0.05$). The mean dispersal direction from the home plant was 202.7° ± 18° (Fig. 1). There was consistently no wind in the morning, and afternoon wind samples had a mean wind angle of 175° ± 10° (Fig. 1).

Weevil dispersal patterns from the home plant in experiment 2 were not random (Rayleigh Test, r [mean vector] = 0.7943, $P < 0.001$). In contrast to the nonrandom weevil dispersal data, the distribution of flowering *Yuccas* about the home plant was random (Rayleigh Test, r [mean vector] = 0.00382, $P > 0.90$). The dispersal pattern of weevils did not

TABLE 1. The mean dispersal distance of weevils released from different home plants. The mean dispersal distance of weevils found at each type of target plant type is listed for each experimental period; *n* represents the number of weevils recovered. Distance is in meters ± 1 standard deviation.

		Rosette to which weevils dispersed		
Home plant type	*n*	Nonflowering	Young flowering	Old flowering
First experiment				
Nonflowering	75	0	33 ± 8 m	0
Flowering	4	0	15 ± 2.5 m	0
Second experiment				
Nonflowering	26	0	18 ± 11 m	0

match the expected pattern of flowering *Y. whipplei* dispersal (chi-square test, $\chi^2 = 87.5$, df = 7, $P > 0.05$). However, there was a good relationship between wind direction and weevil dispersal direction (chi-square test, $\chi^2 = 6.5$, df = 7, $P < 0.05$).

In both experiments weevils that were released in the morning had not moved by the afternoon sampling period of the same day. All weevils moved between the afternoon sampling session and the following morning session. Two casual observations at dusk showed weevils flying from a nonflowering *Yucca* to a new flowering *Yucca*, directly into the wind in a southerly direction.

Greater numbers of weevils were present on the marked flowering stalks with higher caudex temperatures at all sampling times. For afternoon (1600 h) temperature readings, weevil presence on the stalk increased as a function of mean caudex temperatures ($R^2 = 0.86$, $y = 3.9x - 69$; Fig. 2). This relationship also existed in the morning (0800 h; $R^2 = 0.78$, $y = 3.2x - 46$) and the midday (1200 h) samples ($R^2 = 0.73$, $y = 3.5x - 48$). The stalk temperature did not correlate with any other characteristic of the flowering *Y. whipplei* (inflorescence height, leaf lengths, or rosette diameter).

DISCUSSION

Scyphophorus yuccae consistently moved from nonflowering to new flowering *Y. whipplei* more than 15 m apart in a pattern that was not random but was directly into the wind. These results are consistent with our hypothesis that *S. yuccae* would disperse in a nonrandom pattern within a field consisting of flowering and nonflowering *Y. whipplei*. Yucca weevil dispersal to flowering *Y. whipplei* may be important as each flowering *Y. whipplei* represents a weevil reproductive site that is limited to as few as 2 larvae developing per plant (Huxman and Loik 1996). Dispersal to new flowering *Yuccas* could allow weevils to find an unoccupied reproductive site.

Yucca whipplei has a population of weevils infesting the rosette during the vegetative cycle, but they do not appear to cause damage during this cycle by tunneling. However, when the plant flowers, weevils tunnel and deposit larvae (Huxman and Loik 1996). Waring (1986) found that *Agave palmeri* Engelm. has a chemical defense mechanism to repel *Scyphophorus acupunctatus* during the vegetative cycle of the plant. The defense mechanism is abandoned during the flowering phase. There could be a similar plant defense mechanism in *Y. whipplei* as in *A. palmeri*, and the relaxing of the defense could influence weevil dispersal.

If *Y. whipplei* produces some sort of attractant, production may fade with time as the inflorescence matures. In this study, data from the 1st and 2nd experiments show that differential dispersal to new and old flowering stalks occurred, which suggests that an attractant may be present in earlier stages of inflorescence development and lacking in later stages, although the exact nature of this attractant is unknown. Large amounts of water and soluble sugars flow up the flowering stalk in newly developing floral displays in *A. deserti* Engelm. and sharply decline as resources in the plant diminish (Tissue and Nobel 1990). The same sugar flow may occur in *Y. whipplei*, which has a similar floral display, and it is possible that declining resources may influence weevil dispersal.

Simple directional dispersal with the wind tends to be passive, while flight directly into the wind is considered active (Stein et al. 1994). The dispersal characteristics we measured in

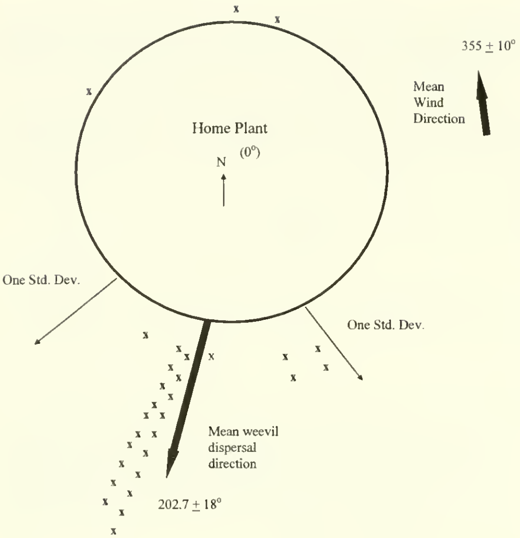

Fig. 1. Physical layout of the plot with respect to weevil dispersal direction from the home plant. Each recovered weevil's dispersal direction is represented by an x. Mean weevil dispersal direction along with standard deviations and mean wind direction are indicated by arrows. Angles are mean ± 1 standard deviation.

the 2nd experiment suggest the weevil is an active disperser that moves directly into the wind. Wind has been shown to be a good predictor of dispersal direction for mountain pine beetles, *Dendroctonus ponderosae* (Safranyik et al. 1989). At certain wind velocities, mountain pine beetles have been shown to fly downwind in the absence of an attractive semiochemical and directly into the wind when an attractant is present (Safranyik et al. 1989). *Scyphophorus yuccae* flies into the wind and can be trapped by using extracts of *Y. whipplei* inflorescence as an attractant (T. E. Huxman unpublished data).

In all 3 experiments yucca weevils flew in the afternoon during elevated ambient air temperatures, suggesting that a critical ambient temperature is required before flight can occur. Safranyik et al. (1989) found that in mountain pine beetles temperature affects the onset and duration of flight and regulates dispersal. Critical temperature in yucca weevils could be approximately 26°C (minimum temperature recorded for afternoon periods). Critical temperatures have been recorded for other flying insects: mountain pine beetle (19°C; Safranyik et al. 1989) and *Belonia saturata* (Libellula), a dragonfly (22°C; Polcyn 1994).

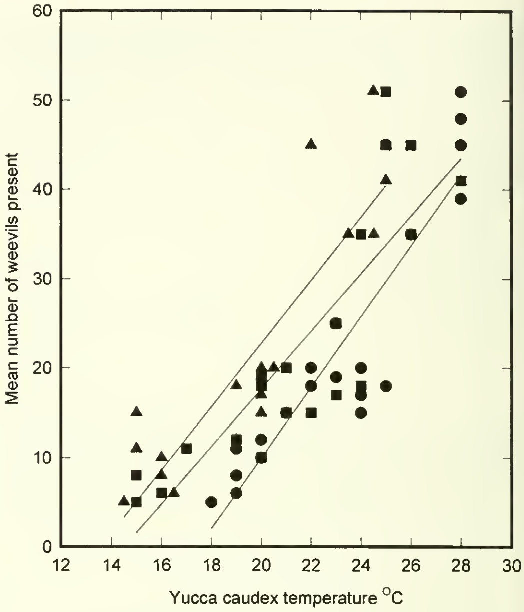

Fig. 2. Regressions of the mean number of weevils present on a rosette to the mean temperature of the caudex of that rosette for 20 marked individuals; ● represents data collected from afternoon samplings, while ■ represents the midday and ▲ the morning. Temperature and weevil population data are plotted as the means of 3 different samplings of the same mapped yucca caudex.

While ambient temperature may be important for flight initiation, our 3rd experiment found that *Y. whipplei* caudex temperature was probably not a dispersal cue for weevils. The nearly constant populations of weevils on *Yuccas* throughout the day regardless of morning versus afternoon mean caudex temperatures (Fig. 2) suggest that weevils may stay on a rosette for thermoregulatory reasons, but they probably do not locate the target plant by temperature. Including temperature as a characteristic to measure in earlier mark-and-recapture experiments would have been beneficial in understanding the role of target plant temperature in dispersal.

Insect dispersal within a heterogeneous landscape is often quite different from movement in a homogeneous plot (Crist et al. 1992). Therefore, dispersal characteristics among the homogeneous distribution of *Y. whipplei* that we observed may be very different from dispersal among plants in the larger scale patchy mosaic. *Yucca whipplei* often forms a clumpy mosaic within the southern San Gabriel Mountains (Haines 1941). *Scyphophorus yuccae* has the ability to disperse within these patches of plants. Long-range dispersal (>50 m) between patches of *Y. whipplei* may be important to the population dynamics of the weevil.

The dynamics of the infestation would be important to understand in determining the evolution of *Y. whipplei's* reproductive habit. Damage caused by reproduction of the weevil on flowering stalks tends to be greater for smaller stalk sizes (Huxman and Loik 1996). Reductions in seed crop production by destruction of the structural integrity of the inflorescence could result in selection for a large floral display (Schaffer and Schaffer 1977). Thus, the yucca weevil may play a significant role in the selection for semelparity in *Y. whipplei*. There is evidence suggesting that the maintenance of an erect inflorescence is important for germination of seeds in *Y. whipplei* (Huxman and Loik 1997), and damage by the weevil may prevent stalks from remaining erect.

Insects in which dispersal and subsequent reproduction can be easily measured provide a good model for the investigation of dispersal effects on population dynamics (Stein et al. 1994). Reproduction can be estimated for yucca weevils by counting the scars on flowering stalks, as a single larva develops for each scar present (Huxman and Loik 1996). In this study we showed that dispersal characteristics are easily measured for yucca weevils. Future studies should include life-table analysis along with dispersal and reproduction to address population dynamics of the weevil. Dispersal characteristics may be important for population dynamics in this weevil because of limitations in reproductive sites. The damage this monophagus weevil causes to an inflorescence and its dispersal may reduce the field seed production of *Y. whipplei* and may be important in understanding the natural history of *Y. whipplei* (Huxman and Loik 1996).

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EVALUATION OF FISH DIPLOSTOMATOSIS IN STRAWBERRY RESERVOIR FOLLOWING ROTENONE APPLICATION: A FIVE-YEAR STUDY

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ABSTRACT.—Strawberry Reservoir, Wasatch County, Utah, was treated with rotenone in August 1990. For 5 yr following treatment, about 2000 fish from 5 different species were examined for eye metacercariae (*Diplostomum*). Incidence dropped from 88.0% before to 0.1% after treatment for cutthroat trout (*Oncorhynchus clarki*), from 93.0% to 0.1% for rainbow trout (*O. mykiss*), and from 19.0% to 10.0% for redside shiner (*Richardsonius balteatus*). Average numbers of metacercariae per eye also dropped from 6.8 to 0.1 for cutthroat trout, from 23.1 to 0.1 for rainbow trout, and from 18.9 to 0.1 for redside shiner. Kokanee salmon (*O. nerka*), introduced into the reservoir 1 yr after treatment, had a 0.9% prevalence rate and average of 0.1 metacercariae per eye. Rotenone affected almost all organisms in the system. Low incidence of diplostomatosis after treatment indicates that rotenone effectively destroyed many intermediate hosts (fish, snails), which in turn probably affected parasite burdens in definitive hosts (gulls). These changes in metacercariae per host probably occurred because of the complex life cycle of the organism, which is similar to other trematodes. Rotenone is a specific inhibitor of electron transport complex 1 and can be devastating to parasites with complex life cycles. Through a combination of factors, parasite numbers have decreased in Strawberry Reservoir.

Key words: rotenone treatment, eye fluke, Strawberry Reservoir, parasite life cycle, Diplostomum.

Eye fluke disease or diplostomatosis is a fish disease caused by strigeoid trematodes (Trematoda: Diplostomatidae) mainly of the genus *Diplostomum.* The disease's first appearance in North America was in the New Jersey State Hatchery at Hackettstown during 1937 and 1938, where it caused considerable damage to several fish species (Palmer 1939). Diplostomatosis was first reported in Utah in Strawberry Reservoir, considered the state's number 1 trout lake (Palmieri et al. 1976). The 1st intermediate hosts for *Diplostomum spathaceum* in Utah are the snails *Lymnaea palustris* and *L. stagnalis* (Palmieri et al. 1976, 1977). The 2nd intermediate host is fish, which occur within several families (Palmieri et al. 1976). The major definitive hosts in Utah are Ring-billed Gulls (*Larus delawarensis*) and California Gulls (*L. californicus*; Evans et al. 1976, Palmieri et al. 1977). Beginning early in spring and continuing through late summer, California Gulls are more prevalent. By September, Ring-billed Gulls predominate in the Strawberry Reservoir area. This causes a change in major definitive hosts from spring to autumn. More than 38 avian species in 7 families have been identified as definitive hosts of *D. spathaceum* throughout the world (McDonald 1969). Palmieri et al. (1976) recorded high prevalence of infection by *D. spathaceum* in salmonids and other fish species inhabiting Strawberry Reservoir, Utah (Table 1), and reported 6.5% and 5.7% infection prevalence in *Lymnaea palustris* and *L. stagnalis*, respectively, throughout the state.

Fisheries management in Strawberry Valley has been influenced by introductions of nongame fish for more than 30 yr. During the late 1950s, Utah chub (*Gila atraria*), Utah sucker (*Catostomus ardens*), carp (*Cyprinus carpio*), and yellow perch (*Perca flavescens*) had nearly displaced trout in Strawberry Reservoir. In October 1961 the reservoir was chemically treated with rotenone to remove undesirable fish. Reservoir volume at that time was 22,661 acre ft and surface area was 3300 acres. Treatment consisted of applying 1249.0 L of rotenone to 88.6 km of tributary streams, 13,247.5 L along the shoreline, and 27,216 kg of rotenone mixed into water-based slurry to the reservoir surface. Rotenone concentration was estimated at 1.77 parts per million (ppm). Total cost of treatment was $43,000. Utah chub reappeared in 1973 and Utah sucker had reestablished by 1978. Sources of these introductions are unknown (Wildlife Resources Division of Utah 1988).

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TABLE 1. Rotenone treatment* for diplostomatosis in 6 fish species from Strawberry Reservoir, Utah, previous to 1990.

Host	Sample size	Percent infection	Average number of metacercariae per host
Oncorhynchus clarki Cutthroat trout	85	88	6.8
Oncorhynchus mykiss Rainbow trout	92	93	23.1
Salvelinus fontinalis Brook trout	7	100	93.7
Catostomus platyrhynchus Mountain sucker	30	100	135.0
Catostomus ardens Utah sucker	11	100	8.8
Richardsonius balteatus Redside shiner	27	19	18.9

*J. R. Palmieri, R. A. Heckmann, and R. S. Evans 1976.

Strawberry Reservoir was again treated with 408,240 kg rotenone to eradicate undesirable fish in August 1990. Rotenone was applied using an "aspirator" on each of the mixing barges. Large 454-kg bags of chemicals were loaded directly onto boats. The chemical was then pulled from the bags with high-pressure pumps that mixed it with lake water as the boats traversed the reservoir. Total cost was around $3.5 million (Daily Herald [Provo, Utah] 1990).

The purposes of this paper are (1) to evaluate the effect of rotenone treatment on diplostomatosis in Strawberry Reservoir and (2) to contribute to a greater understanding of host/parasite relationships in the system.

MATERIALS AND METHODS

Fish were collected from Strawberry Reservoir 3 times a year by the Central Division of Utah Wildlife Resources to assess the state of the fisheries. Eyes of fish in these collections were checked for parasite infection following standard biological evaluation by state fisheries biologists. Approximately 5–10% were examined on site using dissecting microscopes; the remainder were fixed in 70% ethyl alcohol and examined in the laboratory, where each eye was dissected, the lens placed in 1 container, and the vitreous humor and retinal tissue in another container. We recorded which eye(s) were infected and the number and location of parasites. Metacercariae were isolated by location, stained with Semichon's carmine, destained with acid-alcohol, mounted with Permount (Lillie 1991), and identified following the procedure and keys of Shigin (1986).

Eyes from infected fish were processed by standard histological techniques (Sheehan and Hrapchak 1973, Lillie 1991), sectioned at 4–6 μm, and stained with hematoxylin and eosin, Mallory's trichrome, and toluidine blue. Slides were examined with a compound light microscope to evaluate the host/parasite interaction.

RESULTS

During the 5-yr period (1989 and 1992–1995), 3496 eyes from 5 fish species were examined for metacercariae. These included rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*O. clarki*), kokanee salmon (*O. nerka*), redside shiner (*Richardsonius balteatus*), and Utah chub (*Gila atraria*; Table 2). Metacercariae were found infecting the lens, vitreous humor, or both (mixed infections). In eyes examined in situ, metacercariae were actively motile when extracted. Metacercariae in the lens were identified as *D. spathaceum* (Fig. 1); those floating free in the vitreous humor were identified as *D. baeri* (Fig. 2).

Histological preparations did not show alterations in the lens capsule. Metacercariae of *D. spathaceum* were situated near the periphery of the lens and invaded the liquified portion representing that year's growth of tissue (Fig. 3). The number of metacercariae in the lens was low (1–20) for 1992–1995, and the overall infection rate for the 5 fish species was low (0.96%) for 1993–1995. No inflammatory response or retinal detachment was observed associated with *D. baeri* infections (Fig. 4b).

Table 2. Data for fish examined from Strawberry Reservoir, Utah, during 1989 and 1992–1995. Compare with Table 1 (pretreatment levels). Note: 1989 is a pretreatment sample.

Host	Year	Eyes examined		# of eyes infected		%	Mean/meta/eye	
		Fixed	Fresh	Fixed	Fresh	infected	Fixed	Fresh
Cutthroat trout	1989	0	2	0	2	100.0	0.0	4.0
Oncorhynchus clarki	1992	0	86	0	20	23.0	0.0	0.0
	1993	0	82	0	0	0.0	0.0	0.0
	1994	282	34	0	8	0.1	0.0	0.31
	1995	106	340	5	2	0.1	0.1	<0.1
Rainbow trout	1989	0	112	0	25	22.0	0.0	2.13
Oncorhynchus mykiss	1992	0	94	0	14	14.8	0.0	0.0
	1993	0	62	0	0	0.0	0.0	0.0
	1994	608	52	0	4	0.0	0.0	0.21
	1995	170	154	0	3	0.1	0.0	0.1
Kokanee salmon	1992	0	118	0	14	11.8	0.0	0.0
Oncorhynchus nerka	1993	0	10	0	0	0.0	0.0	0.0
	1994	415	22	0	0	0.0	0.0	0.0
	1995	115	0	1	0	0.9	<0.1	0.1
Mix salmonids*	1994	505	0	2	0	0.4	0.1	0.0
Utah chub *Gila atraria*	1994	107	0	0	0	0.0	0.0	0.0
Redside shiner *Richardsonius balteatus*	1994	10	10	0	1	10.0	0.0	0.1
Total		2318	1178	9	93	2.7	0.1	0.5

*Not able to identify species from head samples; no labels in sample bags.

DISCUSSION

Assuming that most fish were eradicated, diplostomatosis has reentered Strawberry Reservoir following rotenone treatment as exemplified by infected fish. However, posttreatment rates are much lower than pretreatment levels (Tables 1, 2). We do not observe a definite pattern in parasite dynamics. This is the first report of *D. baeri* from Strawberry Reservoir.

Rotenone is a well-known pesticide used widely in home gardens. Its use as fish control as part of water-body management is restricted by the Environmental Protection Agency (Ray 1991, Walter and Keith 1992). Rotenone readily breaks down when exposed to sunlight with most of the toxicity being lost in 5–6 d of spring sunlight or 2–3 d of summer sunlight (Walter and Keith 1992). The compound can be neutralized before entering other bodies of water. Rotenone metabolizes rapidly in soil and in water. The half-life of rotenone in both environments is 1–3 d, and the compound does not readily leach from soil; thus it is not expected to be a groundwater pollutant (Walter and Keith 1992). Rotenone is slightly toxic to wildfowl and highly toxic to fish and aquatic invertebrates that have a wide range of sensitivity.

During the treatment of the reservoir the minimum concentration of rotenone obtained was 0.022 ppm (Wildlife Resources Division of Utah 1988). At this concentration most organisms living in or closely related to the reservoir were affected. Fish eradication was considered successful, and detoxification of the reservoir occurred in the estimated time. During the rotenone treatment period, birds consumed dead fish. No documentation is available about the effect of rotenone on birds, mollusks, and other invertebrates during the treatment period at Strawberry Reservoir. Nishiuchi and Yoshida (1972) found that rotenone caused contraction in snails, and almost all died after 3–4 d in test water. Because the minimum concentration of rotenone was above lethal levels for almost all aquatic organisms (Anonymous 1991), we assume most intermediate hosts for *Diplostomum* spp. were eliminated.

Pretreatment infection rates for salmonids ranged from 80% to 100% (Evans et al. 1976, Palmeri et al. 1976). Following treatment, salmonids were restocked in the reservoir. All fish used for stocking came from Utah state fish hatcheries, most of which are diplostomatosis-

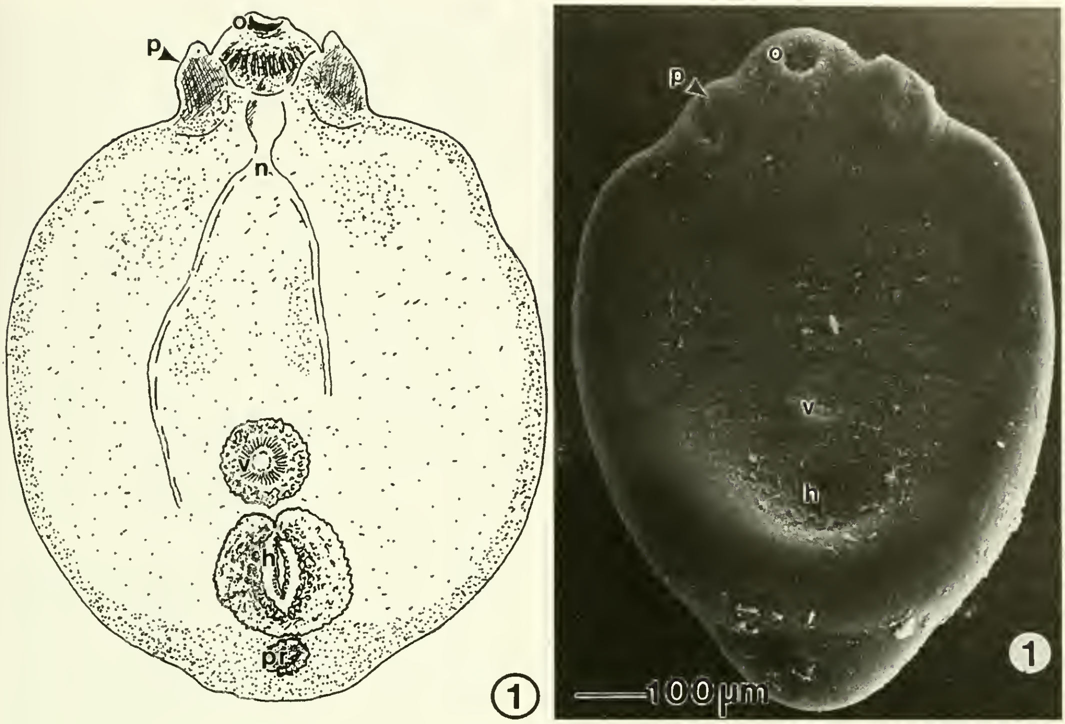

Fig. 1. Line drawing and SEM micrograph of metacercariae of *Diplostomum spathaceum* in the lens of fish from Strawberry Reservoir, Utah: h = holdfast, n = blind intestine, o = oral sucker, p = pseudo sucker, pr = primordium, v = ventral sucker. Bar = 100 μm.

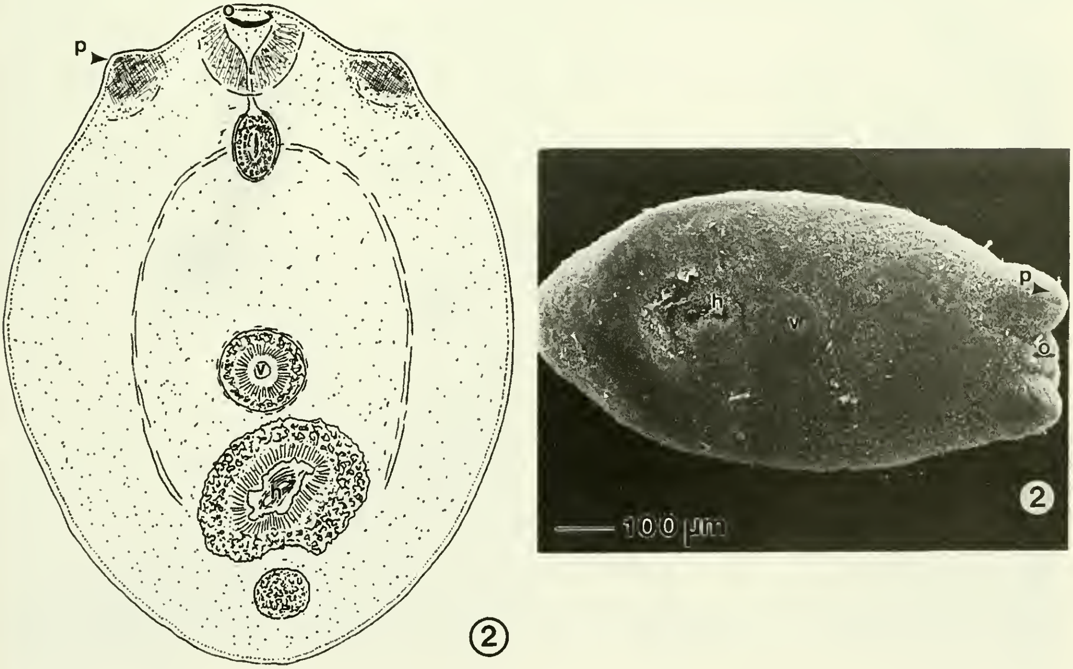

Fig. 2. Line drawing and SEM micrograph of metacercariae of *D. baeri* in the vitreous humor of fish from Strawberry Reservoir, Utah: h = holdfast organ, o = oral sucker, p = pseudo sucker, v = ventral sucker. Bar = 100 μm.

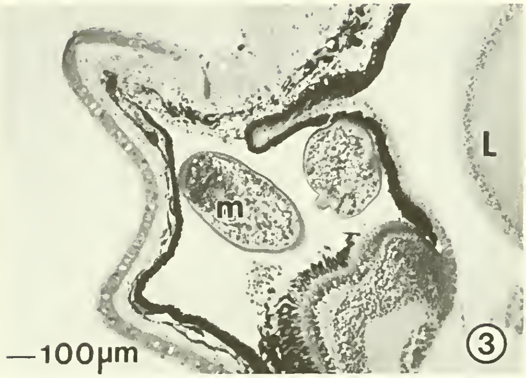

Fig. 3. Metacercariae (*D. spathaceum*) infecting the lens of fish: L = lens, m = metacercariae. Note the separation of the retinal layer from the choroid layer. Mag. 400X. Bar = 100 μm.

free. From 1990 to 1994, 15,234,362 cutthroat trout, rainbow trout, and kokanee salmon were reintroduced into Strawberry Reservoir (Central Division, Utah Division of Wildlife Resources, personal communication). Stocking was to reestablish a quality sport fishery. Four years after the treatment, nongame fish such as Utah chub and redside shiner were captured in the reservoir. Incidence of diplostomatosis is still low compared to pretreatment levels (Table 2); however, due to reservoir size and the abundance of (intermediate and definitive) hosts, diplostomatosis may again reach a high prevalence.

Palmieri et al. (1976) and Evans et al. (1976) noted that *D. spathaceum* had only 2 molluscan intermediate hosts and 2 definitive avian hosts in Utah. Because no further data are available for this area, we do not know all the dynamics of the parasite/host relationship prior to treatment in 1990. A possible source of reestablishing the *Diplostomum* life cycle in Strawberry Reservoir is nearby streams and lakes. There also is a chance that reintroduced fish were carriers of the parasite.

Major definitive hosts in Utah are Ring-billed Gulls and California Gulls. Beginning early in the spring and continuing through late summer, the California Gull is most prevalent. From September the Ring-billed Gull predominates until the reservoir ices. This accounts for a constant supply of *Diplostomum* eggs from spring to fall each year. Because of the

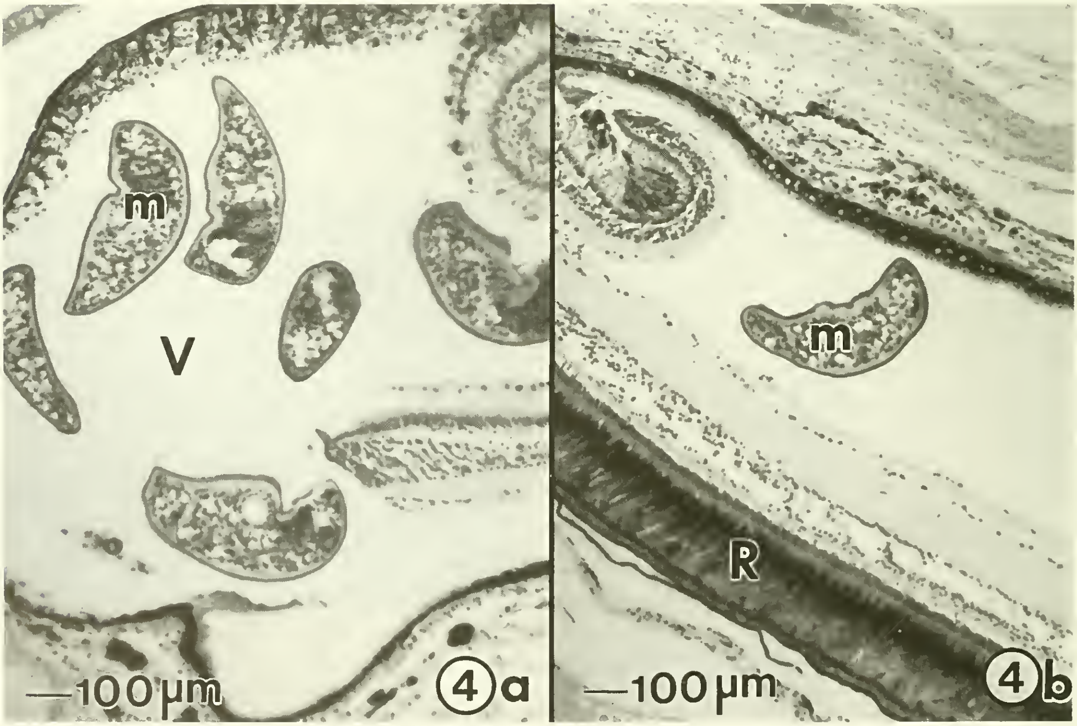

Fig. 4. Metacercariae (*D. baeri*) floating free in the vitreous humor of the infected fish (4a) and next to the retina (4b): m = metacercariae, R = retina, V = vitreous humor. Mag. 400X. Bar = 100 μm.

abundance of dead fish during the treatment period, seagulls, mainly California Gulls, ate an unusually large amount of fish and may also have suffered toxic effects of the rotenone (Feldman and Kruckenberg 1975). Even though no data are available, the possibility exists that rotenone reached the birds' intestines and affected the parasites there. Because the treatment was done during late August, the Ring-billed Gull was probably the most affected. We assume that all stages in the parasite life cycle were somewhat altered.

Inasmuch as most fish reintroduced into the reservoir were from parasite-free hatcheries, the parasite will require some time to become established in these fish. The sample of cutthroat trout for 1989 was only 2 fish, both of which were infected. Rainbow trout for that year had an infection rate of 22%, which dropped to 0% during subsequent years. An explanation for these data may be that fish planted in the reservoir following treatment came from hatcheries, such as the Midway, Utah, fish hatchery, which has earth-lined raceways. Earth-lined raceways are conducive to establishing the life cycle of *Diplostomum*. The fish may have been infected with *Diplostomum* metacercariae previous to planting in the reservoir.

Diplostomum spathaceum metacercariae were in the liquified portion of the lens, and the pathology correlates with reactions described by Shariff et al. (1980). Infections in the lens of the fish are visible for 1 yr, after which the infected lens tissue changes color and absorbs the fluke (Palmieri et al. 1977). Histological studies showed no alterations caused by *D. baeri* found in the vitreous humor or adjoining epithelial tissue and retina for this study. After 1990 there were very few infected fish in the reservoir, indicating a lack of reestablishment of the cycle. It would be advantageous to start long-term studies on the parasitic disease for fish in Strawberry Reservoir to evaluate host/parasite dynamics and to record future changes in the infection.

ACKNOWLEDGMENTS

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HUMAN TRAMPLING EFFECTS ON REGENERATION AND AGE STRUCTURES OF *PINUS EDULIS* AND *JUNIPERUS MONOSPERMA*

Alex S. Tonnesen[1,2] and James J. Ebersole[1,3]

ABSTRACT.—We examined effects of human foot traffic on age structures and densities of seedlings and saplings of *Pinus edulis* (Colorado pinyon) and *Juniperus monosperma* (one-seed juniper) in a heavily used urban park, Garden of the Gods, Colorado. Age structures show no stand-destroying disturbances, but they do contain small peaks 85–95 yr ago (minimum age), which have been interpreted as responses to heavy grazing. For *Pinus edulis* reverse J-shaped age structures indicate a strongly reproducing population, while flat age structures of *J. monosperma* show low present reproduction. Young trees showed strong preferences for establishing under existing trees and shrubs and not among herbs or on bare soil. *Pinus edulis* seedling density was reduced by 73% in heavily trampled areas compared to lightly trampled areas. However, there were no differences in density when only the area protected by rocks, shrubs, or trees was considered. This indicates that direct effects such as physical damage and soil erosion kill young trees, and indirect effects, such as lower seed production, do not cause the lower densities in heavily trampled areas. *Pinus edulis* saplings and *J. monosperma* seedlings and saplings showed no differences in density across trampling intensities. In heavily trampled areas of Garden of the Gods Park, recent increases in use have apparently reduced *Pinus edulis* seedling establishment enough that long-term regeneration is threatened. Managers of all pinyon-juniper woodlands must recognize that in areas strongly impacted by foot traffic, and also presumably by similar disturbances such as vehicle traffic, sufficient regeneration likely does not occur to replace trees. The areal extent of severely disturbed areas should be limited, and managers should seek to avoid further degradation of less damaged areas.

Key words: pinyon-juniper woodland, Pinus edulis, Juniperus monosperma, *trampling, disturbance, recreation ecology, management, age structure, seedling, microsite preference, regeneration.*

Pinyon-juniper woodlands cover large areas of western North America and are important for wildlife, recreation, occasionally firewood (West 1988), and for Native American uses (Wasson 1987, Jebsen-Ross and Schwab 1995). Much of the research in pinyon-juniper woodlands has focused on expansion of the community and increases in tree density since the 1800s (Jameson 1962, Blackburn and Tueller 1970, Burkhardt and Tisdale 1976, Tausch et al. 1981, West 1984, Miller and Wigand 1994, Miller and Rose 1995). Other research has studied disturbance to cryptogamic soil crusts in this community (Johansen and St. Clair 1986, Cole 1990, Beymer and Klopatek 1992, Belnap 1993). No study has addressed the effects of recreational disturbances upon age structures and recruitment of pinyons and junipers.

Here we examine effects of trampling from human foot traffic in a heavily used park adjacent to an urban area. In parts of the study site, trampling has removed most understory vegetation and caused substantial soil erosion. With such obvious effects on grasses and forbs, we focused on trees to determine if trampling has affected dominant plants of the ecosystem as well. Our results may apply to other pinyon-juniper woodlands and other disturbances, such as vehicle use, that remove herbaceous plant cover.

Specifically, our goals were to (1) determine how varying intensities of trampling have affected seedling and sapling densities of *Pinus edulis* Engelm. (Colorado pinyon) and *Juniperus monosperma* (Engelm.) Sarg. (one-seed juniper), (2) use age structures to determine the length of time this disturbance has affected tree establishment, and (3) predict future trends in these woodlands.

STUDY AREA

Garden of the Gods is a 553-ha city park on the edge of Colorado Springs, Colorado. The first portion of the park, including the study site, was established in 1909 (Colorado Springs

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Parks and Recreation Department 1986, 1994), when grazing was presumably stopped.

The park straddles transitions from plains to foothills and from grasslands to woodlands of *Pinus edulis* and *Juniperus monosperma*. *P. edulis* and *J. monosperma* reach their northeastern and northern limits, respectively, at Colorado Springs, with the exception of a few disjunct populations of *P. edulis* (Little 1971, Weber 1976). Mature *P. edulis* individuals substantially outnumber mature *J. monosperma* individuals even though *J. monosperma* is normally more common at lower elevations (Woodin and Lindsey 1954, Lajtha and Getz 1993). *Cercocarpus montanus* (mountain-mahogany) and *Quercus gambelii* (Gambel oak) are the most common shrubs of these woodlands.

The climate is semiarid with a 30-yr mean precipitation of 41 cm/yr recorded at a site 17 km to the east-southeast and 80 m lower. Winters are dry and mild with a mean January temperature of –2°C. Summers are warm (July mean temperature 22°C), with frequent thunderstorms that create a summer precipitation peak (NOAA 1993).

Study sites are located on the strongly dipping portion of the Fountain Formation; they have eastern to southern aspects, flat to 32° slopes, and elevations of 1940 to 2000 m. Soils are of the Connerton series, deep, well-drained loams with gravel (Soil Conservation Service 1981). Surface runoff on study plots is medium to rapid, erosion hazard is moderate to high, and the sites have moderate to severe limitations for recreation (Soil Conservation Service 1981).

Over 1 million visitors per year visit this relatively small park (Colorado Springs Parks and Recreation Department 1994). Large numbers of people leave maintained trails, creating an obvious network of social trails and general trampling that very few areas have escaped. Areas close to trails, parking areas, and prominent rock outcrops retain little understory vegetation, and soil erosion is severe. In the most severely eroded areas, shrubs are on pedestals 0.5–1 m tall, and vertical-sided erosion gullies measuring up to 4 m deep have been cut. Trees in these areas, and even in areas moderately affected, commonly have partially exposed roots.

Invasive species and species resistant to trampling due to low stature (Liddle 1991), such as *Bouteloua* spp. (Ebersole unpublished data), make up most of the herbaceous cover remaining on heavily trampled sites. Areas with relatively dense herbaceous cover (40–75%) comprise approximately 5% of the pinyon-juniper community and are limited to areas that are farther from roads and trails and are blocked from easy access by very steep slopes or rock outcrops. These areas are dominated by plants less resistant to grazing (Risser et al. 1981) and presumably to human trampling due to their higher stature (Liddle 1991), such as *Andropogon gerardii* (big bluestem), *Schizachyrium scoparium* (little bluestem), and *Bouteloua curtipendula* (sideoats grama). Most of the pinyon-juniper community has received moderate levels of disturbance and has an understory of 12–35% cover.

METHODS

We considered 3 trampling intensities defined by cover of herbaceous vegetation: lightly trampled, >35% cover; moderately trampled, 11–35% cover; and heavily trampled, ≤ 10% cover. Areas with bedrock close to the surface and drainages were not sampled, and all plots had very similar soils.

Between August and October 1992, we estimated ages of 75–120 individuals of both *P. edulis* and *J. monosperma* within both moderately and heavily trampled areas. There was not enough lightly trampled area to sample. The largest possible rectangular plots, up to 20 m by 40 m, were placed in homogeneous areas; all trees with greater than 7-cm basal diameter were cored 15–20 cm above the ground; and rings were counted.

In cores without centers, distance to the center was determined and age adjusted using average inner ring width of cores with centers. No attempt was made to account for missing years or false rings. Since missing rings are common in pinyon and especially juniper, absolute ages are likely underestimates (Despain and Klemmedson 1987). However, we assumed missing rings occurred with approximately the same frequency in different trampling intensities. Ages were not adjusted for height of coring aboveground. They are an estimated 15–20 yr older than reported based on Tausch and West's (1988) findings that seedlings of *Pinus monophylla* (singleleaf pinyon) and *Juniperus osteosperma* (Utah juniper) 8–12 cm tall were 10–15 yr old.

Trees too small to core were grouped into 3 size classes: (1) seedlings (basal diameters <0.5

TABLE 1. Median, minimum, and maximum ages (yr) of small and large saplings of *Pinus edulis* and *Juniperus monosperma* determined by basal cross section. Samples were obtained 3 km south of the primary study site (see Methods).

	Small saplings				Large saplings			
	n	Median	Minimum	Maximum	*n*	Median	Minimum	Maximum
Pinus edulis	8	14.5	9	29	8	26.5	18	40
Juniperus monosperma	9	18	11	42	9	42	24	62

cm), (2) small saplings (basal diameters of 0.5–7 cm and <50 cm tall), and (3) large saplings (basal diameters of 0.5–7 cm and ≥ 50 cm tall). Ages of saplings were estimated by counting rings of similar-sized individuals cut at ground level within the same plant community, aspects, bedrock, and elevation 3 km south of Garden of the Gods. Seedlings were assumed to be ≤ 10 yr (Blackburn and Tueller 1970).

Microsite locations and densities of seedlings and saplings were determined from belt transects in October 1995. Ten plots, each 4 m by 20 m, were placed into each trampling regime: light, moderate, and heavy. All live seedlings and saplings were tallied by location: under trees, under shrubs, next to rocks, on bare soil, or within herbaceous vegetation. If normality assumptions were met, densities were compared with ANOVA; if not, Kruskal-Wallis tests were used. Homoscedasticity was not tested since *P* values are not affected by inequality of variance if sample sizes are equal (Scheffé 1959).

Midlines of belt transects were used for line-intercept sampling to determine areal proportions of the 5 microsites. Mean proportions of each microsite within each disturbance intensity were used to calculate expected numbers of seedlings and saplings assuming a random distribution. For chi-square tests rock, shrub, and tree counts were combined as sites protected from trampling, so that expected values met criteria of Koehler and Larntz (1980) for minimum expected frequencies.

RESULTS

Basal cross sections of saplings (Table 1) showed large variation in age, with *J. monosperma* generally older than *Pinus edulis* of similar size. Age structures (Fig. 1) are graphed with small and large saplings in the equivalent positions of 10–19 and 20–29 yr. Since saplings showed moderate to strong tendencies to be older than this (Table 1), age classes with midpoints of 35–65 yr will be substantially to slightly increased over the number obtained from cores, and the apparent number of trees 10–29 yr will be decreased (Fig. 1).

Under both trampling regimes *Pinus edulis* showed reverse J-shaped age structures, with moderately large numbers of young relative to older trees (Fig. 1). Age distributions of the 2 disturbance intensities do not differ significantly ($P = 0.23$). Since areas sampled differ between disturbance regimes, absolute densities cannot be inferred and compared from Figure 1.

J. monosperma age distributions were flatter than those for *P. edulis* (Fig. 1). Because many saplings are older than 29 yr (Table 1), in moderately trampled areas there are fewer individuals in the youngest age classes than in age classes around 85 yr. In heavily trampled areas *J. monosperma* seedlings appeared to be more abundant than individuals in older age classes, but saplings, after corrections from Table 1, were less abundant than individuals in age classes around 95 yr. Age structures in the 2 trampling regimes are different ($P = 0.009$) due to the larger number of seedlings and saplings and the fewer older trees in heavily disturbed areas (Fig. 1).

Absolute density of *Pinus edulis* seedlings was reduced 73% in heavily trampled areas compared to lightly trampled areas (Fig. 2, $P = 0.02$). Moderately disturbed areas showed intermediate *P. edulis* seedling densities although they were not significantly different from the 2 other trampling intensities. Densities of *P. edulis* saplings and of *Juniperus monosperma* seedlings and saplings combined did not differ among the 3 disturbance regimes (Fig. 2). When considering only sites protected by rocks and woody plants, trampling intensity does not change densities of seedlings and saplings (Table 3). Although the means for *P. edulis* seedlings suggest a trend, this is due to 1 high-density outlier in a lightly trampled area.

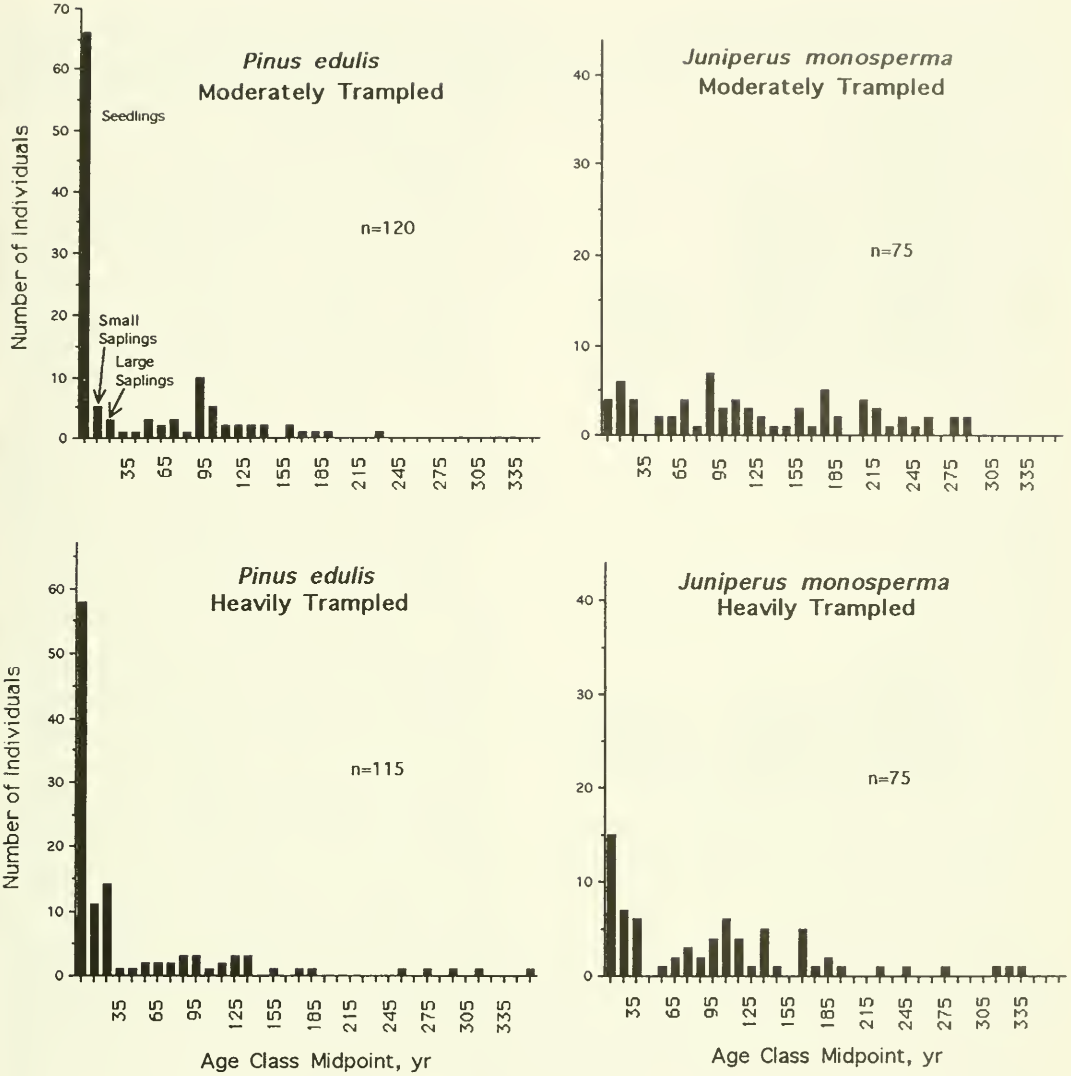

Fig. 1. Age structures of *Pinus edulis* and *Juniperus monosperma* under moderate and heavy trampling. Lengths of y-axes are proportional to sample size so bars of equal height represent the same relative frequency. In all graphs, seedlings and saplings are the left 3 bars as indicated in the first graph. Ages of destructive samples of seedlings (≤ 0.5 cm basal diameter), small saplings (basal diameter 0.5–7 cm and <50 cm tall), and large saplings (basal diameter 0.5–7 cm and ≥ 50 cm tall) are given in Table 1. *P. edulis* age distributions are not different (P = 0.23, two-sample Kolmogorov-Smirnov test for large sample sizes [Sokal and Rohlf 1995: 434]), and for *J. monosperma* they are different (P = 0.009).

Pinus edulis seedlings and saplings showed similar strong preferences for microsites, and these preferences were consistent across trampling intensities (Table 2). Fewer individuals than expected based on random distributions were found on bare soil; and more than expected were found in sites protected by rocks, shrubs, and trees. Because rock cover was very low, preferences were for sites under shrubs and trees. *J. monosperma* tended to show the same microsite preferences, although the rarity of young individuals made significance tests impossible (Table 2).

DISCUSSION

Reverse-J age distributions of *Pinus edulis* and the lack of fire scars on trees indicate no stand-destroying disturbances in the past 350 yr. Small peaks at 85–95 yr before sampling in

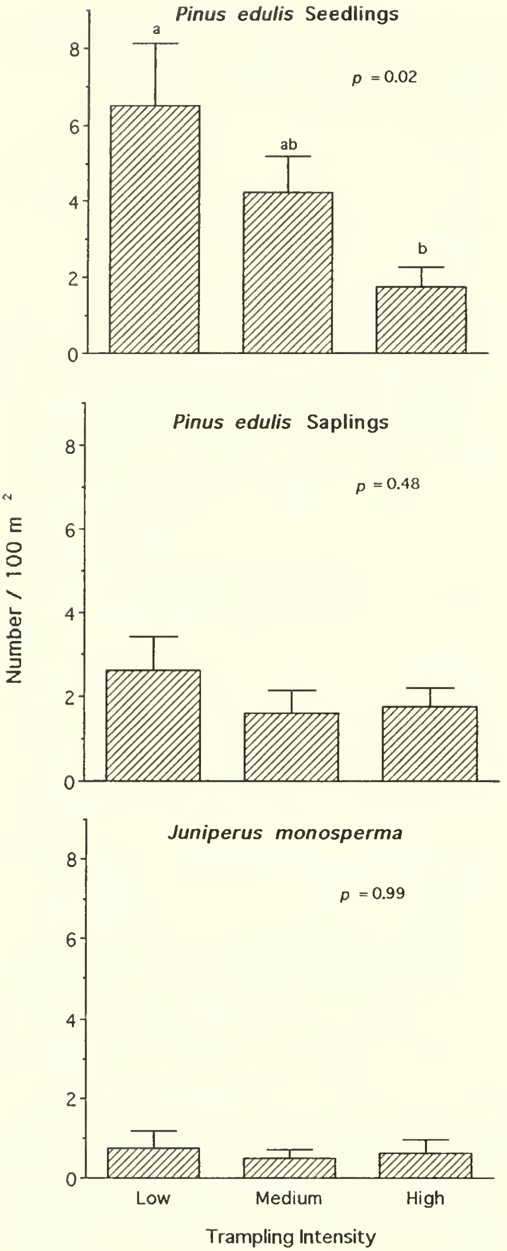

Fig. 2. Densities ($\bar{x} \pm s_{\bar{x}}$, $n = 10$) of *Pinus edulis* and *Juniperus monosperma* seedlings and saplings under 3 trampling intensities. The 2 sapling sizes of *P. edulis* and all seedlings and saplings of *J. monosperma* were combined to obtain sufficiently large samples. Significance of one-way ANOVAs (square root transform for *P. edulis* saplings) or Kruskal-Wallis test (for *J. monosperma*) is given as *P* values. Means with the same letter are homogeneous subsets (Tukey's test of all pair-wise comparisons, experiment-wise $\alpha = 0.05$).

3 of 4 cases (Fig. 1) may be the result of overgrazing that reduced fine fuels and fire frequency as hypothesized by Burkhardt and Tisdale (1976), Miller and Wigand (1994), and Miller and Rose (1995).

Preference of young pinyons and junipers for microsites protected by woody plants has been found by others (Phillips 1909, Tausch et al. 1981, Welden et al. 1990, Miller and Rose 1995) and is likely caused here by (1) reduced soil surface temperatures compared to bare soil and soil under grasses (Burkhardt and Tisdale 1976); (2) frost heaving of seedlings being more common on bare soil (Heidmann 1976); (3) protection under woody plants from direct injury of trampling; (4) scrub jays avoiding caching *P. edulis* seeds in open areas (Balda 1987; pinyon jays are uncommon in Garden of the Gods); and (5) perhaps defecation of juniper seeds by birds perched in trees. Lack of density differences among trampling regimes within protected sites (Table 3) indicates that direct effects such as soil erosion and physical injury from foot traffic reduce densities of young trees. If indirect effects such as decreased seed production in heavily trampled areas were important, then protected sites of heavily trampled areas would presumably show lower densities.

The sharp decrease in density of *Pinus edulis* seedlings caused by trampling and the lack of density differences for *P. edulis* saplings (Fig. 2) imply trampling has limited seedling establishment only recently. Apparently, the marked growth in users and subsequent trampling in Garden of the Gods over the last decades (personal observation, Beidleman written communication) has substantially increased seedling mortality.

Management Implications

In pinyon-juniper woodlands with heavy human trampling, and presumably similar disturbances caused by heavy vehicle use, loss of understory vegetation is obvious. Erosion rates are also greatly increased, by approximately 10–35 times relative to undisturbed areas (Wilcox 1994). In addition to these more obvious effects, this study provides strong evidence that in heavily trampled areas insufficient regeneration occurs to replace trees as they die. Managers must realize that these heavily impacted areas are sacrifice areas not being used sustainably. It is important to limit the

TABLE 2. *Pinus edulis* and *Juniperus monosperma* observed and expected seedling and sapling frequencies by microsite. There were ten 4 × 20 m plots in each trampling intensity. To meet minimum expected frequencies for χ^2, 2 sizes of *Pinus edulis* saplings were combined; and rock, shrub, and tree microsites were considered together as protected sites (data are also given by original 5 microsites). *J. monosperma* seedlings and saplings were combined, and no statistical tests were done due to small expected frequencies.

	Average % cover	*P. edulis* seedlings			*P. edulis* saplings			*J. monosperma*	
		Obs	Exp	χ^2/P	Obs	Exp	χ^2/P	Obs	Exp
LIGHTLY TRAMPLED									
Bare	31.4	3	12.9	39.73	4	6.6	12.25	0	1.9
Herb	36.9	12	15.1	0.000	3	7.8	0.002	1	2.2
RST[a]	31.4	37	12.9		14	6.6		5	1.9
Rock	2.1	4	0.9		2	0.4		1	0.1
Shrub	5.7	13	2.3		1	1.2		1	0.3
Tree	23.6	20	9.7		11	5.0		3	1.4
Total		52			21			6	
MODERATELY TRAMPLED									
Bare	45.6	0	21.4	50.60	0	5.9	11.18	0	1.8
Herb	24.3	5	11.4	0.000	5	3.2	0.004	1	1.0
RST	30.4	29	14.3		8	3.9		3	1.2
Rock	0.6	1	0.3		2	0.1		0	0.0
Shrub	15.3	14	7.2		5	2.0		0	0.6
Tree	14.5	14	6.8		1	1.9		3	0.6
Total		34			13			4	
HEAVILY TRAMPLED									
Bare	67.2	1	9.4	25.55	4	9.4	14.24	1	3.4
Herb	5.9	1	0.8	0.000	0	0.8	0.000	1	0.3
RST	26.9	12	3.8		10	3.8		3	1.3
Rock	0.6	0	0.1		0	0.1		0	0.0
Shrub	15.2	6	2.1		9	2.1		1	0.8
Tree	11.2	6	1.6		1	1.6		2	0.6
Total		14			14			5	

[a]Rock, shrub, and tree microsites combined

TABLE 3. Densities (no./m^2, $\bar{x} \pm s_{\bar{x}}$, $n = 10$) of *Pinus edulis* and *Juniperus monosperma* seedlings and saplings in protected sites (rock, shrub, and tree microsites combined). Significance of Kruskal-Wallis tests for differences among trampling regimes is given.

	Trampling intensity			
	Light	Moderate	Heavy	*P*
P. edulis seedlings	0.31 ± 0.162	0.12 ± 0.024	0.06 ± 0.019	0.18
P. edulis saplings	0.052 ± 0.018	0.040 ± 0.015	0.048 ± 0.018	0.92
J. monosperma	0.023 ± 0.016	0.018 ± 0.013	0.025 ± 0.019	0.94

areal extent of these heavily impacted areas by controlling use, and managers should also seek to prevent lightly and moderately impacted areas from deteriorating further. *Pinus edulis* and *Juniperus monosperma* are not only the most visually dominant species of this community, but they also hold soil in place, modify the environment for many other plant species (West 1984), and provide food and cover for many animals (Sedgwick and Ryder 1987). Their substantial reduction or loss would markedly reduce the biological and recreational values of these woodlands.

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ECOPHYSIOLOGY OF THE TEMPERATE DESERT HALOPHYTES: *ALLENROLFEA OCCIDENTALIS* AND *SARCOBATUS VERMICULATUS*

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ABSTRACT.—Numerous basins of the intermountain area often have extensive playa surfaces that are nearly devoid of vegetation. Margins of these playas support sparse communities dominated by the chenopod shrubs *Allenrolfea occidentalis* (iodine bush) and *Sarcobatus vermiculatus* (black greasewood). These plants establish and persist in an environment where halomorphic soils induce extreme osmotic stress and atmospheric precipitation is very low and erratic and occurs largely during the winter when temperatures are too low for growth. We measured net CO_2 assimilation rates, leaf conductances, transpiration rates, water-use efficiencies, and stem xylem potentials for these two C3 species. Data were collected in above-average (1991) and below-average (1992) precipitation years. Net CO_2 assimilation rates for *Allenrolfea* were statistically similar in 1991 and 1992 but in general declined for *Sarcobatus* in 1992. For both species, leaf conductances and leaf transpiration rates declined significantly from 1991 to 1992, with the decline significantly greater for *Sarcobatus*. Water-use efficiencies doubled from 1991 to 1992 for both plant species. Predawn xylem water potentials were –2.2 and –3.3 MPa for *Allenrolfea* and –1.8 and –2.6 MPa for *Sarcobatus* beginning in May 1991 and 1992, respectively, and dropped to –3.8 and –4.2 MPa for *Allenrolfea* and –1.8 and –2.8 MPa for *Sarcobatus* by September 1991 and 1992, respectively. Afternoon xylem water potentials were –3.1 and –2.0 MPa for *Allenrolfea* and –2.6 and –2.2 MPa for *Sarcobatus* beginning in May 1991 and 1992, respectively. Xylem water potentials dropped to –5.0 MPa for *Allenrolfea* and –3.4 MPa for *Sarcobatus* by September of both 1991 and 1992. For *Allenrolfea*, in general, the total soil water potential within the zone of maximum root activity is more negative than the plant's predawn xylem potential, which suggests that the plant is partially phreatophytic and/or has a large capacitance due to its extensive woody root system.

Key words: iodine bush, black greasewood, photosynthesis, conductance, transpiration, water potential, water-use efficiency, salt desert.

The vast pluvial lakes that occupied the basin of the intermountain area during the Pleistocene (Russell 1885) exposed extensive lake plains to colonization by plants as the waters evaporated during the late Pleistocene. Halomorphic soils, wind erosion, and atmospheric aridity hindered colonization of these environments (Billings 1945, 1949, West 1983). Lower portions of these basins remain nearly free of vegetation as barren playa surfaces. Margins of these playas currently limit plant colonization. Communities of shrubs dominated by Chenopodiaceae characterize much of the pluvial lake plain environment (Billings 1949). Apparently, these shrubs and half-shrubs have undergone explosive evolution in successfully exploiting the lake plain environments (Stutz 1978). The North American endemic chenopods *Sarcobatus vermiculatus* (Hook.) Torr. (black greasewood) and the monospecific *Allenrolfea occidentalis* (S. Wats) Kuntz (iodine bush) have colonized extremely saline habitats of these temperate desert basins (Young et al. 1995). *Sarcobatus*, found in numerous plant communities in temperate deserts (e.g., Billings 1945), is moderately salt tolerant and can survive at the low end of the moisture gradient in salt desert communities (Skougard and Brotherson 1979). *Sarcobatus*, which employs the C3 photosynthetic carbon reduction pathway, can be phreatophytic if the groundwater table is high enough (Robinson 1958, Rickard 1965, Groeneveld 1990). *Allenrolfea*, also a C3 (scanning electron microscopy of leaf section did not show structures indicative of C4 pathways), is much more restricted in ecological amplitude, being limited to a few communities directly at the margin of playas where soils are often poorly drained, have high surface soil salinity, but are non-sodic (Shantz 1940, Skougard and Brotherson 1979).

The purpose of this study was to determine plant strategies that allow *Allenrolfea* and *Sarcobatus* to survive, indeed flourish, in this harsh, extremely saline playa margin environment. Our working hypothesis postulated that roots of *Sarcobatus* tap shallow, lower osmotic potential groundwater, while roots of *Allenrolfea* primarily seek moisture from the eolian mounds on which they are found. This hypothesis was tested by studying plant-soil relationships and measuring plant ecophysiological attributes for *Allenrolfea* and *Sarcobatus* over 2 yr. Fortuitously, the years differed markedly in precipitation, which provided insight into water acquisition.

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METHODS

The study site is in Eagle Valley, an embayment of pluvial Lake Lahontan, near the Hot Springs Mountain Range about 80 km northeast of Reno, Nevada (119°15′W, 39°45′N, 1234 m). The landscape consists of a lake plain rising in a series of small (>1 m) escarpments bordering a large playa. A band of large (>10 m) sand dunes forms a disjunct arc across the lake plain. *Allenrolfea* forms a very sparse community, with plants located on low mounds (0.1–0.5 m high) on a former playa surface. Occasional *Sarcobatus* and/or *Atriplex lentiformis* ssp. *torreyi* (Torrey saltbush) share mounds with the smaller *Allenrolfea*. Discontinuous colonies of *Distichlis spicata* (desert saltgrass) are the only herbaceous vegetation found in the communities. Mounds and intermound soils are extremely saline (Tables 1, 2) and consist of coarse-textured eolian material overlying clay- and silt-rich lacustrine sediments remnant of pluvial periods of Lake Lahontan (Blank et al. 1992). The high osmotic potential of the soil seedbed limits new plant recruitment (Blank et al. 1994).

Prior to the studies, 8 perforated PVC tubes were installed throughout the study area to monitor the water table. The tubes extended to a depth of 3 m. Measurements were taken monthly throughout 1991 and 1992. A sample of the groundwater was returned to the laboratory and electrical conductivity (EC) determined using a salinity drop tester; total water potential was measured on selected samples using a Decagon DC-10 thermocouple psychrometer (mention of trade names does not imply endorsement by the USDA).

Separate studies were conducted in 1991 and 1992. The 30-yr average annual precipitation for this region is 11.5 cm (Reed 1941). In 1991 and 1992 the study area received 14.6 cm and 9.6 cm of precipitation, respectively (based on rain gauges at the study site). Thus, plant-water relations and carbon exchange were measured in above-average and below-average precipitation years. In the 1st study diurnal measurements (6–8 measurements from sunrise to sunset) of net photosynthesis, leaf conductance, transpiration, relative humidity, leaf temperature, and photosynthetically active radiation (PAR) were taken with an LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE) equipped with a 0.25-L leaf chamber. Plots (4 blocks) were randomly selected that contained both *Allenrolfea* and *Sarcobatus*, and ecophysiology measurements were taken by block on 10 July, 2 August, and 25 September 1991 and on 10 July, 8 August, and 23 September 1992. To facilitate measurements, stems containing several leaves were inserted into the chamber. After measurement stems were harvested and returned on ice to the laboratory where leaf areas were measured. *Allenrolfea* ecophysiological measurements were based on cylindrical leaf area, as stomata appeared to cover the entire leaf. *Sarcobatus* measurements were based on a 1-sided flat leaf because in the samples we examined stomata occurred only on the hairy and flattened leaf surface.

In the 2nd study more intensive afternoon ecophysiology measurements were taken. Measurements were taken as mentioned above in the diurnal study; however, we measured predawn and afternoon stem xylem potentials with a Scholander-type pressure chamber. Measurements were taken on 30 April, 10 June, 8 July, 30 July, and 23 September 1991 and 20 April, 27 May, 26 June, 16 July, 7 August, and 23 September 1992.

In August 1991 we determined rooting depth and root length density for *Allenrolfea* by digging into 4 mounds occupied exclusively by *Allenrolfea*. Roots were collected at depths of 0–30, 30–60, 60–90, 90–120, and 120–150 cm. The volume of soil taken was 3780 cm^3. Soil was washed from roots in tubs and organic debris was picked from the roots. Root length was determined using a Comair root length scanner (Hawker de Havilland, Salisbury, South Australia). A subsample of roots were stained with a congo red solution (congo red stains dead roots) and examined with a light microscope to determine the proportion of dead roots, which was then used to correct root length density.

To prepare samples of *Allenrolfea* for scanning electron microscopy, we immediately

TABLE 1. Pedon descriptions and selected attributes of mound occupied by *Allenrolfea occidentalis.* Mound is near where the ecophysiological measurements were taken.

							Saturated paste						
Horizon	Depth (cm)	Munsell color	pH	Sand	Silt	Clay	Na^+	Cl	SO_4^{-2}	Ca^{+2}	Mg^{+2}	K^+	NO_3^-
				percent			mmol						
Av	0–1.5	2.5Y 6/3	7.8	78.8	7.1	14.1	990	960	33.0	57.8	3.2	7.3	6.61
C1	1.5–20	2.5Y 6.5/2	8.1	75.6	12.6	11.7	540	550	12.7	5.9	1.3	5.9	0.05
C2	20–76	2.5Y 6.5/2	8.3	85.7	5.8	8.5	310	300	43.1	27.3	2.9	4.6	0.49
By	76–86	2.5Y 6/2	8.0	nd	nd	nd	270	280	41.6	18.9	2.0	4.0	0.08
C3	86–122	5Y 6/3	5.2	68.0	16.0	16.0	380	410	12.3	12.3	3.3	3.4	0.01
2C	122–157	2.5Y 7/2	8.0	48.2	28.0	23.8	160	170	16.5	4.6	0.9	2.6	0.11
2Cg	157+	2.5Y 7/2	8.1	8.1	54.9	37.0	120	140	6.5	2.3	0.5	3.2	0.02

TABLE 2. Selected mean anion and cation values from saturation extracts taken at 2–10 cm from 4 microsites (6 replicates) and from groundwater samples (4 replicates) at the Eagle Valley study site.

Microsite	Chloride	Sodium	Sulfate	Potassium	Nitrate
	mmol				
Bare mound	1580	1450	39	66	8.1
Allenrolfea	600	690	63	102	3.3
Sarcobatus	1460	1340	40	24	4.4
Groundwater	220	200	12	14	0.06

placed freshly excised leaves in a solution of 5% glutaraldehyde, 25% polyethylene glycol, and 10% acetone. After 1 wk we dehydrated the leaves using a graded series of alcohol and then critical-point-dried them prior to observation.

Near the time diurnal and afternoon measurements were taken, we collected soil at depths of 20, 40, and 60 cm from mounds (6 replicates) near where plant measurements were taken. Though the mounds were largely occupied by *Allenrolfea*, some samples were taken from mounds occupied by both species. We immediately placed the soil in a sealed glass vial and returned it to the laboratory. In the laboratory the samples were homogenized and total soil water potential was determined with a Decagon SC-10 thermocouple psychrometer. The extreme salinity of samples required instrument calibration using a series of saturated salt solutions.

The data were analyzed as a split-block in time using SAS analysis of variance (ANOVA) models. In the 1st experiment the data were analyzed by year and month to determine species and diurnal effects on physiological parameters. The species effect was tested by the species × block interaction term while the diurnal effect was tested by the overall error mean square. In the 2nd experiment, data were analyzed by year to determine the species and monthly effect on physiological parameters. Similar error terms were selected as in the 1st experiment. A probability value of $P \leq 0.05$ was used throughout the analyses to test significance of F values. Only significant differences are reported in the text. When significant interactions occurred between main effect means, only those judged to have ecological significance were interpreted.

RESULTS

Measurements were taken on cloudless days, so the PAR perpendicular to the sun reached approximately 2000 μmol m^{-2} s^{-1} by about 1030 h for all measurement dates. Values of net CO_2 assimilation, leaf conductance, and leaf transpiration depend on leaf area, which for these 2 species is difficult to unambiguously define. For this reason we will concentrate on diurnal, seasonal, and yearly changes by species in these values.

Net CO_2 assimilation rates were generally highest in the late morning and decreased slightly through the rest of the day (Fig. 1). In general, for equivalent diurnal seasonal

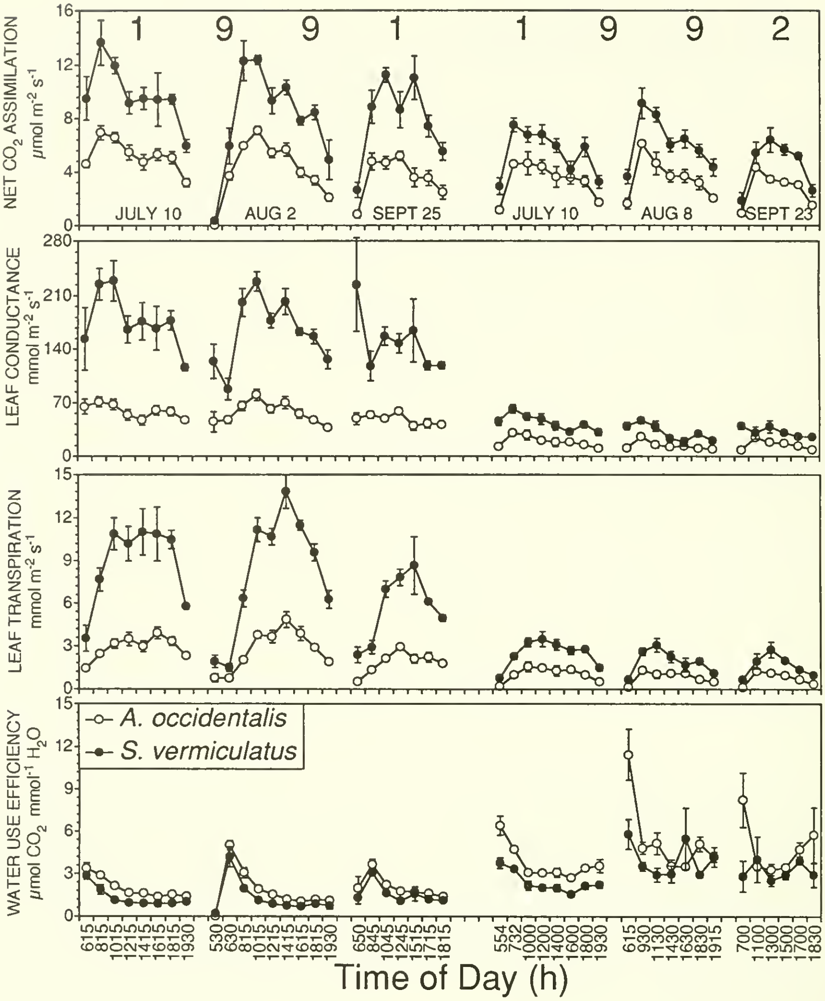

Fig. 1. Diurnal measurements of net carbon dioxide assimilation, leaf conductance, leaf transpiration, and water-use efficiency for *Allenrolfea occidentalis* and *Sarcobatus vermiculatus* in 1991 and 1992. Error bars for this and following figures are standard errors about the means.

measurement dates, rates were significantly higher for both plant species in 1991 (wet) than in 1992 (dry); however, a similar pattern was not evident in the more comprehensive afternoon data set (Fig. 2). In 1991 net CO_2 assimilation was highest in midsummer, whereas in 1992 there was no significant trend with season (Fig. 2).

For the first 2 dates in 1991, leaf conductance was generally highest in the morning and decreased in the afternoon, with a slight increase again by late afternoon (Fig. 1). This pattern was not evident in the 25 September 1991 diurnal measurement. Leaf conductance for both *Sarcobatus* and *Allenrolfea* was significantly less in 1992 than in 1991 (Figs. 1, 2). Moreover, the differences in leaf conductance between *Allenrolfea* and *Sarcobatus* were significantly less in 1992 than in 1991 (Figs. 1, 2). In 1991 leaf conductance varied significantly by time of day for *Sarcobatus*, but a diurnal pattern was more mute in 1992 (Fig. 1). Leaf transpiration rates followed the same trends as leaf conductance (Figs. 1, 2).

Water-use efficiency of *Allenrolfea* was significantly greater than *Sarcobatus* for all measurement dates in 1991 and 1992, with the exception of the 25 September 1991 measurement (Fig. 1). Water-use efficiencies in 1991 for both plants were significantly less than in 1992.

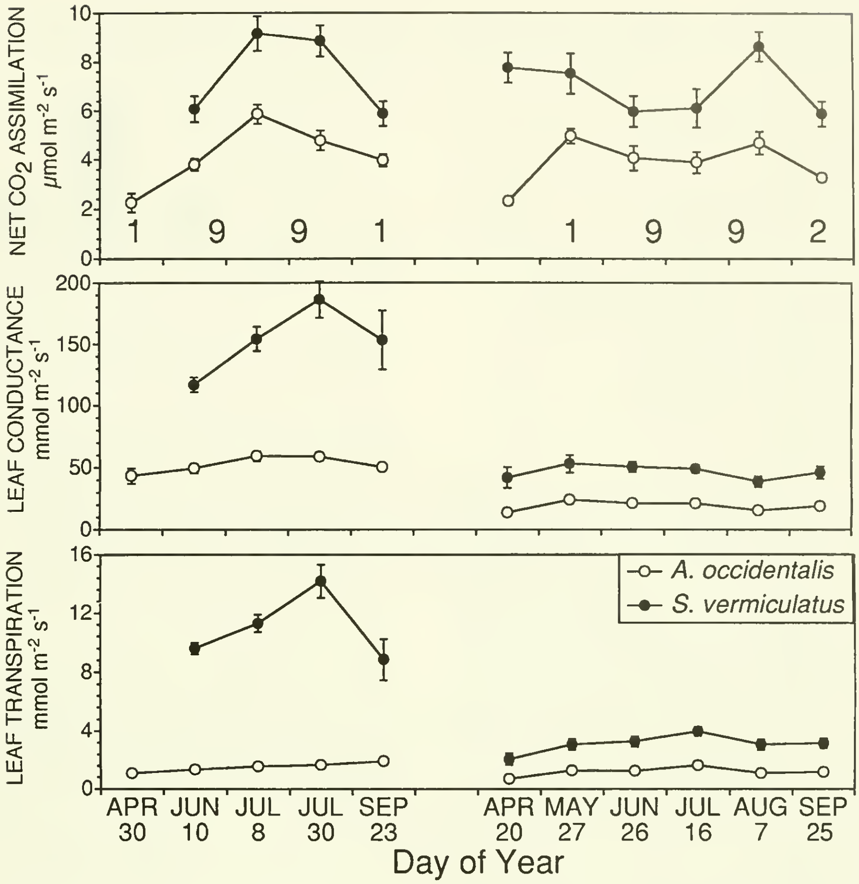

Fig. 2. Afternoon measurements of net carbon dioxide assimilation leaf conductance and leaf transpiration for *Allenrolfea occidentalis* and *Sarcobatus vermiculatus* in 1991 and 1992.

In 1991 and 1992, *Allenrolfea* had significantly more negative afternoon and predawn stem xylem potentials than *Sarcobatus* (Fig. 3). Soil water potentials remained between –15 and –20 MPa at the 20-cm depth for 1991 and until August 1992 when they dropped to –40 to –50 MPa (Fig. 3). In 1991 soil water potentials at 40 cm actually increased from about –11 MPa to –7 MPa from May to July and decreased to –5 MPa by late September. In 1992, however, the soil water potential at 40 cm was about –6 MPa from April to July and then dropped to –20 MPa by August. There were no significant differences in leaf temperature between plant species for 1991, the above-average precipitation year (Fig. 3). In 1992, the dry year, afternoon leaf temperatures of *Sarcobatus* were consistently higher than those of *Allenrolfea.*

Allenrolfea produces the greatest quantity of its roots at 30–60 cm in the hummock, with a small quantity of its roots occurring down to 120–150 cm (Fig. 4). Studies of the rooting density of *Sarcobatus* indicate it exponentially declines with depth (Groeneveld 1990).

Changes from an above-normal precipitation year (1991) to a below-normal precipitation year (1992) are reflected in the depth to the water table (Table 3). By summer 1992 the water table had dropped below 3 m for all access tubes. The EC data also show that groundwater is much less saline than is the soil solution in the soil above (see Tables 1, 2).

DISCUSSION

Leaf conductance and transpiration of the chenopod shrubs *Sarcobatus vermiculatus* and

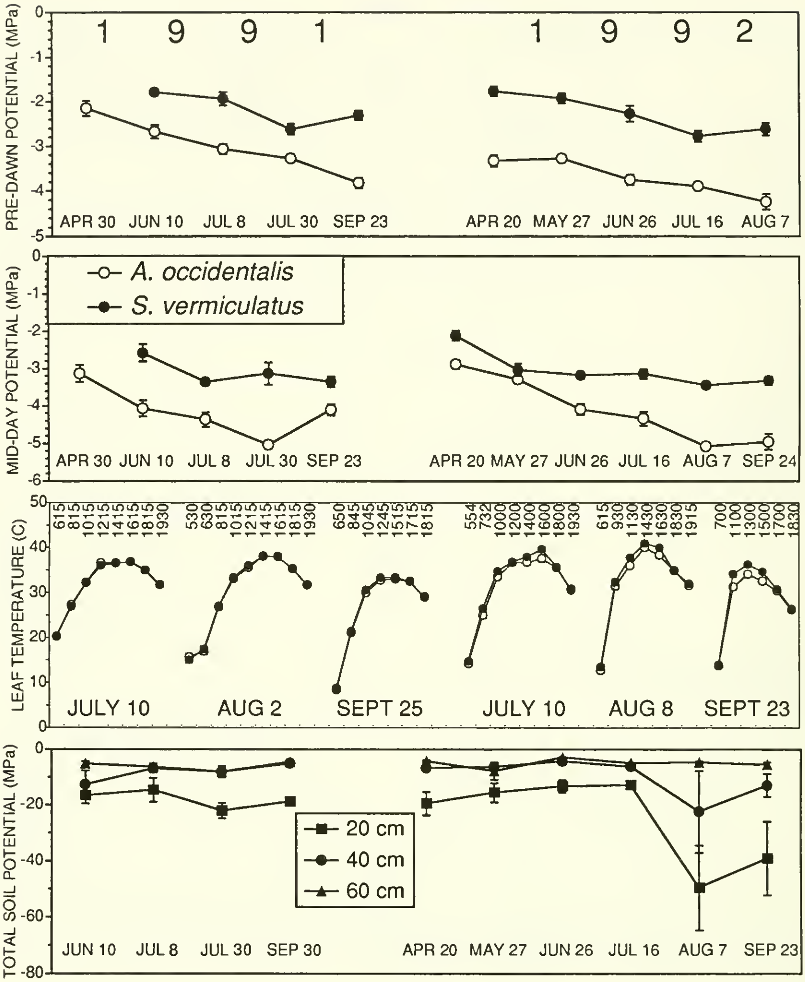

Fig. 3. Predawn and afternoon xylem potentials and diurnal leaf temperatures by sampling date in 1991 and 1992 for *Allenrolfea occidentalis* and *Sarcobatus vermiculatus* and total soil water potentials at depths of 20, 40, and 60 cm below top of hummock for growing seasons in 1991 and 1992.

Allenrolfea occidentalis declined to a greater extent than net assimilation of CO_2 from the above-average precipitation year (1991) to the below-average precipitation year (1992). These data indicate that stomatal conductance does not directly correlate with net photosynthesis in these species. The decrease in transpiration and conductance from the wetter to the drier year is in support of Antlfinger and Dunn (1983), who stated that high transpiration rates and conductances in an environment of low water potential and high salinity would have a great impact on salt balance and tissue hydration of the plant species. In this study reduced conductance and transpiration in the dry year may have been fundamental to maintaining tissue hydration of these salt desert plant species. Although we did not measure the water potential of the protoplast compartment, osmoregulation is important in maintaining cell hydration for halophytic species in wet or dry years (Kramer and Boyer 1995).

We suspect that the plant physiological changes from the wet to dry year may be partially explained by an increase in soil salinity. Flanagan and Jefferies (1988) reported that as salinity increased, photosynthesis in *Plantago maritima* declined from 17 to 14 μmol m^{-2} s^{-1} while leaf conductance dropped markedly from 370 to 172 mmol m^{-2} s^{-1}. In their study water-

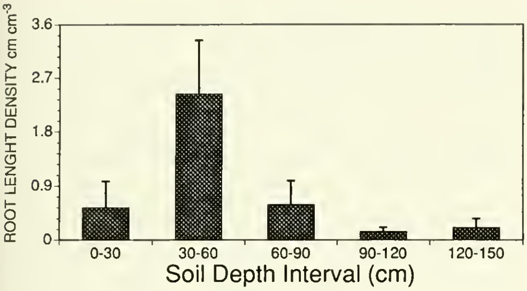

Fig. 4. *Allenrolfea occidentalis* live root length density by depth below top of hummock.

use efficiency increased from 5.7 to 8.5 mmol CO_2 mol^{-1} H_2O, similar to our trend from a wet to a dry year.

Increased soil salinity cannot fully explain the dramatic decreases in leaf conductance from a wet to a dry year. Kleinkopf and Wallace (1974) showed that net assimilation rates and transpiration were not reduced for the salt-tolerant species *Tamarix ramosissima* when salinity increased from 10 to 200 mmol. Pearcy and Ustin (1984) suggested that increased salinity primarily reduced photosynthesis within the mesophyll and secondarily as a result of reduced leaf conductance. Our data show a slight reduction in photosynthesis with a much larger reduction in leaf conductance.

TABLE 3. Water table depth and electrical conductivity (EC) from PVC access tubes. Standard deviations provided in parentheses.

Year Month	Depth (m)	EC (dS m^{-1})
1991		
Jan	2.1 (.3)	23 (7)
Feb	1.8 (.4)	21 (10)
Mar	1.8 (.4)	20 (8)
Apr	1.9 (.4)	20 (5)
May	1.7 (.3)	19 (4)
Jun	1.9 (.2)	19 (5)
Jul	1.9 (.2)	18 (3)
Aug	2.1 (.2)	21 (10)
Sep	2.2 (.3)	19 (3)
Oct	2.5 (.4)	25 (7)
Nov	nd[a]	nd
Dec	nd	nd
1992		
Jan	nd	nd
Feb	nd	nd
Mar	nd	nd
Apr	nd	nd
May	nd	nd
Jun	>3.0	nd
Jul	>3.0	nd
Aug	>3.0	nd
Sep	>3.0	nd
Oct	>3.0	nd
Nov	>3.0	nd
Dec	>3.0	nd

[a] Data not determined during this period.

The effect of soil water potential on photosynthesis, conductance, and transpiration from the 1st (wet) and the 2nd (dry) year is inconclusive. Based on monitor wells at the study site, the water table dropped significantly from 1991 to 1992 and was below 3 m for much of the 1992 season. Since *Sarcobatus* is a facultative phreatophyte (Romo and Haferkamp 1989), and it likely extends roots to at least this depth (Groeneveld 1990), a drop in the water table could explain its reduced transpiration and conductance in 1992. The decline in transpiration and conductance from 1991 to 1992 for *Allenrolfea* is perplexing. Root distribution of *Allenrolfea* suggests it obtains most of its water from within the mound it grows on; yet, the total soil water potential within the mound did not change appreciably during the growing seasons from 1991 to 1992. Indeed, even during the wet year the total soil water potential measured in mounds where maximum root length of *Allenrolfea* occurs was generally more negative than the midday xylem water potential. One possibility is that a small number of *Allenrolfea* roots have tapped into the lowering water table; it is probably a facultative phreatophyte like *Sarcobatus.* During the course of this study, several *Allenrolfea* mounds and adjacent interspaces were excavated. From these excavations it is evident that there is an extensive network of coarse, woody roots of *Allenrolfea.* Samples of large roots have nearly 120 rings, which may constitute annual rings. The moisture content of coarse, woody roots averaged 67% by weight when measured in the spring before appreciable plant growth. These findings suggest that the water relations of *Allenrolfea* may involve a large root capacitance factor.

An alternative explanation of reduced CO_2 assimilation, conductance, and transpiration rates and more efficient water use from 1991 to 1992 involves nitrogen. When moisture is available in surface soil horizons, plants can uptake sufficient, likely luxuriant, inorganic nitrogen owing to plentiful levels in the soil (Tables 1, 2). However, as available moisture in the upper soil profile declines as it did during the dry year of 1992, a plant obtains a greater fraction of water needed from lower soil horizons closer to or within the water table. Inorganic nitrogen levels decline as the water table is approached, which suggests that plants may become deficient in nitrogen (Table 2). Khan et al. (1994) determined that additions of nitrate-N to saline substrates significantly increased carbon assimilation, transpiration, stomatal conductance, and water-use efficiency in alfalfa.

As compared to *Sarcobatus*, *Allenrolfea* exhibited significantly lower stomatal conductance in the wet year 1991 in addition to having, in general, higher water-use efficiency in 1991 and 1992. High water-use efficiency in *Allenrolfea* is partly a function of an extremely rugose epidermal layer in which the stomata are recessed (Fig. 5). The thick boundary layer caused by the rugose surface contributes to lowered stomatal conductance and higher water-use efficiencies (Kramer and Boyer 1995).

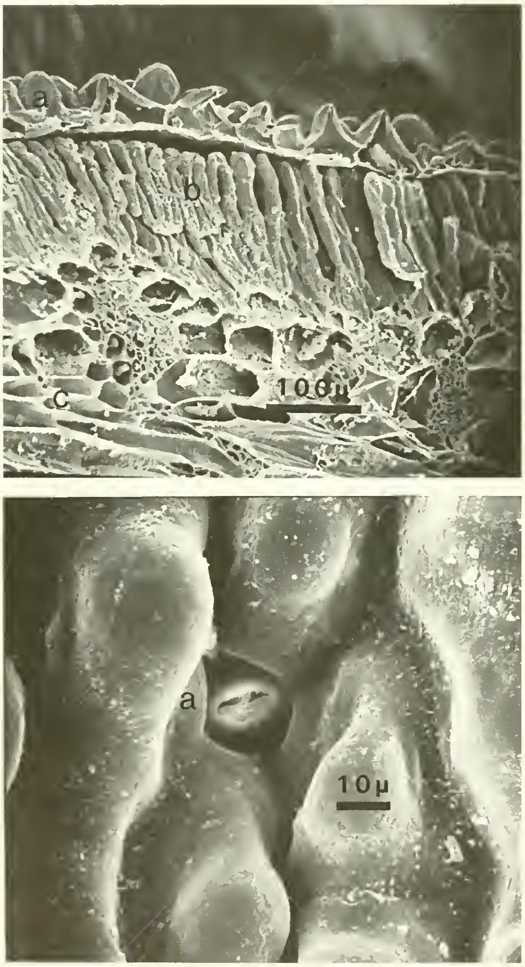

Fig. 5. Scanning electron micrographs of *Allenrolfea occidentalis* leaves. Top micrograph is leaf cross section showing very rugose epidermal layer (a), palisade cells (b), and conductive elements (c). The rugose surface promotes a thick boundary layer above the sunken stomata (a) as shown in the bottom micrograph.

Allenrolfea and *Sarcobatus* maintain similar leaf xylem potentials from a low-precipitation year with a water table depth remaining above 3 m to a dry year when the water table drops below 3 m. A decrease in leaf conductance best explains the maintenance of leaf xylem potentials in the dry 2nd year. Decreased water loss as a result of lowered stomatal resistance should maintain xylem potentials.

In conclusion, *Allenrolfea* and *Sarcobatus* have reduced net assimilation rates, conductances, and transpiration rates during a low-precipitation year. A drop in water table depth, possibly in combination with reduced nitrogen uptake by the plants, explains these results. In high-precipitation years, abundant soil moisture results in high net assimilation rates, high conductance, and high transpiration rates. These years of high soil moisture result in low water-use efficiencies. In contrast to this, plants have the ability to reduce leaf conductance and increase water-use efficiencies in low-precipitation years. This allows the plants to maintain predawn and afternoon water potentials, which vary little from high- to low-precipitation years in these saline environments.

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ASIAN TAPEWORM (*BOTHRIOCEPHALUS ACHEILOGNATHI*) IN NATIVE FISHES FROM THE LITTLE COLORADO RIVER, GRAND CANYON, ARIZONA

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ABSTRACT.—Examination of gastrointestinal tracts of native cyprinids from the Little Colorado River (LCR) in Grand Canyon, Arizona, 1990–1994, revealed varying rates of prevalence and infrapopulation levels of Asian tapeworm (*Bothriocephalus acheilognathi*). Mean prevalence was 28% (range 0–78%) in humpback chub (*Gila cypha*) and 8% (range 0–46%) in speckled dace (*Rhinichthys osculus*), with infrapopulations as high as 46 and 28, respectively. We also note Asian tapeworm infection of the nonnatives common carp (*Cyprinus carpio*), fathead minnow (*Pimephales promelas*), and plains killifish (*Fundulus zebrinus*) from the LCR. Reported pathogenic and chronic effects of this cestode to its definitive hosts add concern for the status of the Grand Canyon population of the federally endangered humpback chub. The rapidity with which Asian tapeworm has spread to different drainages of the Colorado River Basin likely portends an eventual cosmopolitan basin distribution in lower elevations suitable to the parasite's thermophilic life history. Such biotic changes must be considered among the most serious threats to conservation and recovery of native fish populations.

Key words: Bothriocephalus acheilognathi, *parasitism,* Gila cypha, Rhinichthys osculus, *Little Colorado River, conservation.*

During this century, extinctions, extirpations, and declines of native fishes in the American Southwest have been attributed to introductions of nonindigenous fishes and physical habitat alterations (Miller 1961, Minckley and Deacon 1968, Minckley and Douglas 1991). Fish translocations also may introduce pathogens and parasites (Hoffman and Shubert 1984). Introduction and spread of Asian tapeworm (*Bothriocephalus acheilognathi*) to the Colorado River Basin provides an example of the potential effects of such parasite translocations on native fishes. This cestode was first detected from the basin in minnows from the Virgin River, Arizona, Nevada, and Utah, in 1979 (Heckmann et al. 1986). Heckmann et al. (1987, 1993) later reported it from 2 Virgin River tributaries, Beaver Dam Wash, Arizona, and Muddy River and other Nevada localities. Recently, Asian tapeworm has been reported from the Colorado River (CR) and tributaries in Grand Canyon, Arizona (Brouder and Hoffnagle in press), in the San Juan River in Utah and New Mexico (J. J. Landye, U.S. Fish and Wildlife Service, personal communication), and in the Green River in Utah (T. E. Chart, Utah Division of Wildlife Resources, personal communication).

We report Asian tapeworm temporal and numeric infection patterns in 2 native cyprinids from the Little Colorado River (LCR) in Grand Canyon, Arizona. The LCR is the major spawning and early life rearing habitat of the largest remaining population of the federally endangered humpback chub (*Gila cypha*) in the Colorado River Basin (Kaeding and Zimmerman 1983). Speckled dace (*Rhinichthys osculus*) is a geographically widespread native species that codominates the LCR fish assemblage with humpback chub. We also present tapeworm prevalence data for the nonnative cyprinids fathead minnow (*Pimephales promelas*) and common carp (*Cyprinus carpio*), and the cyprinodontid plains killifish (*Fundulus zebrinus*). We examine implications of Asian tapeworm translocation on conservation and recovery of native fishes in the Colorado River Basin.

METHODS

The LCR was sampled in 1991–1994 from the confluence with CR upstream approximately 15 km, where we collected primarily early life stage fishes for stomach content analyses. We also accessed unpublished 1989–1990 LCR data from the Arizona Game and Fish

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Department. Sampling in 1991–1994 was primarily by seine and dip net, while earlier collections also included trammel, gill, and hoop net captures of larger fish. Fish were measured to total length (mm) and preserved in 10% formalin immediately following capture. Larvae and early postlarvae were identified to species using keys of Snyder (1981) and Snyder and Muth (1990). Gastrointestinal (GI) tracts were excised in the lab, where contents were identified and enumerated when possible. Relative volumes of GI tract content categories were visually estimated. J. J. Landye of the U.S. Fish and Wildlife Service (personal communication 1991) made the initial identification of this distinctive tapeworm, and it was later confirmed using Mitchell's (1994) key.

RESULTS

The first observation of Asian tapeworm in the LCR was from 2 subadult humpback chub collected in May 1990 (Minckley 1990). None of the 24 age-1+ humpback chub (>100 mm total length), 3 age-0 juveniles (51–100 mm), 12 postlarvae (26–50 mm), and 6 larvae (<26 mm) examined from 1989 were infected. During 1990, 92.5% of age-0 (including larvae) and 44.4% of age-1+ specimens harbored tapeworms (Table 1). We did not detect Asian tapeworm in the 1991 humpback chub cohort until it approached 50 mm in total length beginning in September. Prevalence in 1992 was 48% overall, but the tapeworm was not found in larval humpback chub. We recorded the parasite in 1 of 62 early life stage humpback chub examined in 1993, and the parasite was absent from 107 larvae examined in 1994 (Table 1).

Asian tapeworm occurrence in speckled dace also was greatest in 1990 at 46%; prevalence in 1991–1993 ranged from 5% to 14% (Table 1). The cestode was absent from early life stages of speckled dace examined in 1994.

Fathead minnow harbored Asian tapeworm in 6 of 75 specimens (8%) collected between 1991 and 1994 (Table 1). Single specimens of plains killifish ($n = 21$) and common carp ($n = 4$) were found infected during this period. The parasite was not found in 480 bluehead sucker (*Pantosteus discobolus*), 71 flannelmouth sucker (*Catostomus latipinnis*), 21 channel catfish (*Ictalurus punctatus*), or 2 rainbow trout (*Oncorhynchus mykiss*) examined from 1990 to 1994.

Tapeworm infrapopulations (mean number per infected fish) in humpback chub GI tracts were 3.7 for larvae ($n = 23$), 3.5 for postlarvae ($n = 15$), 6.9 for age-0 juveniles ($n = 67$), and 10.4 for age-1+ specimens ($n = 12$). Maximum numbers observed in humpback chub were 12 in larvae, 9 in postlarvae, 44 in age-0 juveniles, and 46 in age-1+ specimens. Tapeworms accounted for a mean relative volume of GI tract contents of 51% (maximum 100%) in infected humpback chub.

Infrapopulations in speckled dace were 0.5 ($n = 2$) in larvae (<19 mm total length), 5.3 ($n = 10$) in juveniles (19–50 mm), and 3.5 ($n = 32$) in adults (>50 mm), while maximum densities were 1, 18, and 28, respectively. Relative volume of tapeworms in infected speckled dace averaged 38%. Tapeworm infrapopulations were 2 ($n = 6$; 6 maximum) in fathead minnow (17% relative volume), 3 ($n = 1$) in common carp (<1% relative volume), and 7 ($n = 1$) in plains killifish (100% relative volume).

DISCUSSION

Seasonal (or ontogenetic) and annual differences in prevalence of Asian tapeworm in humpback chub and speckled dace presumably reflect complex interactions among environmental conditions and intermediate (cyclopoid copepod) and definitive host populations (Granath and Esch 1983a, 1983b, Riggs and Esch 1987, Marcogliese and Esch 1989). Infrapopulation dynamics of the parasite may be related to temperature, temperature-dependent rejection responses, immune responses, host distributions, density-dependent factors, or other poorly studied phenomena (Granath and Esch 1983a).

Pathological effects of Asian tapeworm on fish hosts may include intestinal abrasion and disintegration, loss or separation of gut microvilli and enterocytes (Hoole and Nisan 1994), or blockage and perforation of the GI tract (Hoffman 1980, Mitchell 1994). Chronic effects are not well studied but may include the following: emaciation and anemia (Scott and Grizzle 1979); decreases in intestinal, liver, and pancreatic enzymes (Hoole 1994); reduced growth and reproductive capacity, depressed swimming ability via elevated muscle fatigue, and other debilitating influences (Heckmann et al. 1986, Hoole 1994). Weakened fish may develop secondary bacterial infections (Mitchell

TABLE 1. Percent frequency of occurrence (sample size in parentheses) of Asian tapeworm (*Bothriocephalus acheilognathi*) in gastrointestinal tracts of fishes from the lower Little Colorado River, Arizona, 1990–1994. With the exception of larvae, age/stage designations are approximate. Dashes indicate no fish specimens were collected.

	Year				
Species and length	1990	1991	1992	1993	1994
HUMPBACK CHUB					
larvae (≤25 mm)	91.7 (24)	0 (50)	0 (28)	1.8 (56)	0 (107)
postlarvae (26–50 mm)	100 (13)	3.0 (33)	100 (1)	0 (6)	—
older age-0 (51–100 mm)	66.7 (3)	81.2 (32)	67.2 (58)	—	—
age-1+ (>100 mm)	44.4 (18)	37.5 (8)	66.7 (12)	100 (1)	—
SPECKLED DACE					
larvae (≤18 mm)	0 (1)	0 (128)	3.0 (33)	2.8 (36)	0 (95)
juveniles (19–50 mm)	60.0 (10)	4.0 (50)	26.7 (30)	0 (15)	0 (1)
adults (>50 mm)	0 (2)	17.7 (79)	14.4 (111)	50.0 (4)	—
FATHEAD MINNOW					
larvae (≤18 mm)	—	—	0 (4)	—	—
juveniles (19–50 mm)	—	0 (3)	6.9 (29)	0 (4)	0 (3)
adults (>50 mm)	—	0 (2)	8.7 (23)	—	33.3 (6)
COMMON CARP					
juveniles (51–100 mm)	—	—	25.0 (4)	—	—
PLAINS KILLIFISH					
larvae (≤18 mm)	0 (2)	—	—	—	—
juveniles (19–50 mm)	0 (5)	50.0 (2)	0 (8)	—	—
adults (>50 mm)	—	0 (1)	0 (3)	—	—

1994). Granath and Esch (1983c) showed that Asian tapeworm significantly reduced laboratory survivorship of mosquitofish (*Gambusia affinis*) compared to controls, but cautioned that these effects would not necessarily be exhibited in the wild.

More research is needed to determine exact effects of this parasite on native fish populations in Grand Canyon and elsewhere, but clearly Asian tapeworm has the potential to regulate fish populations. The observed patterns of Asian tapeworm prevalence and infrapopulations in humpback chub and speckled dace in the LCR may arise from (1) mortality of hosts with high infrapopulations, (2) density-dependent mortality of parasites, and (3) acquired host resistance to reinfection (Anderson 1982). The fact that our study area is the humpback chub's only major spawning and early life rearing site in Grand Canyon adds concern for the status of this population.

Since its initial detection in the Virgin River in 1979, the rapidity with which Asian tapeworm has spread to different drainages of the Colorado River Basin likely portends an eventual cosmopolitan basin distribution in lower elevations suitable to the parasite's thermophilic life history. Roughly half of the native ichthyofauna in this geographic range comprises cyprinids (Asian tapeworm's most common hosts), with most of those already endangered, threatened, or of special concern. The endangered poeciliid Gila topminnow (*Poeciliopsis o. occidentalis*) of the Gila River subbasin may be vulnerable to this parasite. Because biotic changes to the Colorado River Basin resulting from fish and pathogen translocations are virtually ubiquitous and seemingly irreversible, they must be considered among the most serious threats to conservation and recovery of native fish populations.

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DORALD MERVIN ALLRED
1923–1996

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Dorald Mervin Allred

Dr. Dorald M. Allred, professor emeritus of zoology and entomology, Brigham Young University, Provo, Utah, died 20 June 1996. Born 11 July 1923 in Lehi, Utah, he graduated from Lehi High School and later from Brigham Young University with a Bachelor of Science degree in 1950 and a Master's degree in Entomology in 1951. In 1954 he received a Ph.D. from the University of Utah.

Dorald married Berna Vilate Brown on 14 March 1952. To them were born 5 children, 3 sons and 2 daughters. Dorald was extremely proud of his wife and their family.

After completing his degree at the University of Utah, Dorald served for 2 yr as an entomologist for the U.S. Army at Dugway Proving Grounds. He then joined the zoology faculty at Brigham Young University in 1956, where he served as teacher, researcher, and ecologist for 31 yr. During these years he received many academic and research awards. Among these was Professor of the Year (1958), Karl G. Maeser Research Award (1967), and Certificate of Merit for the Dictionary of International Biology (1970). In addition, Dorald was an officer in the BYU chapter of Sigma Xi during 1973–74, editor of the BYU Science Bulletin for 3 yr, and administrative assistant to the dean of the college before becoming an administrator in the M. L. Bean Life Science Museum (1976) and then its director (1982).

Dr. Allred was a most able teacher, researcher, and administrator. It would be difficult to list him as best at any one. His years as a field biologist, while working under contract for the U.S. Atomic Energy Commission at the Nevada Test Site and at the National Reactor Testing Station in southeastern Idaho, showed his great ability to organize research and survey programs. Considerable information has been cataloged from his field research relating to desert ecology and the numerous invertebrates and vertebrates that live in these desert habitats.

At a critical time in the building of the Bean Life Science Museum, Dorald became assistant director in charge of finance. His experience managing major research contracts prepared him for efficiently utilizing funds allocated for the museum. As director he was most capable in moving academic and public display programs forward.

Aside from his life in academics and education, he served his country in World War II as a communications operator in the U.S. Navy. He was a faithful member of his church and fulfilled many assignments. Dorald had a beautiful tenor voice; and he and Berna, a soprano, provided many hours of enjoyable entertainment for family, academic, and church groups. His talents were numerous and were used liberally not only for his family but also for his friends whenever called upon.

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DISPERSAL OF *JUNIPERUS OCCIDENTALIS* (WESTERN JUNIPER) SEEDS BY FRUGIVOROUS MAMMALS ON JUNIPER MOUNTAIN, SOUTHEASTERN OREGON

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Key words: Juniperus occidentalis, *seed dispersal, mammalian seed dispersal, frugivory, juniper expansion, mammals.*

Juniperus occidentalis Hooker var. *occidentalis* (western juniper, Cupressaceae) covers more than 1 million ha (Miller and Wigand 1994) from south central Washington through eastern Oregon to northeastern California and southwestern Idaho (Adams 1993). Like many other junipers in the West, *J. occidentalis* has undergone extensive recent population expansions, increasing in density and invading downslope into shrub-grasslands. Most believe this juniper expansion has been driven by a combination of climate change, severe overgrazing, and reduced fire frequency (Burkhardt and Tisdale 1976, Eddleman 1987, Miller and Wigand 1994, Miller and Rose 1995; but see Lanner 1977).

The rate and pattern of expansion can be fully understood only with knowledge of seed dispersal, however (Schupp and Fuentes 1995); yet few quantitative studies of dispersal exist for junipers in general (e.g., Livingston 1972, Salomonson 1978, Holthuijzen et al. 1987, Jordano 1993, Chavez-Ramirez and Slack 1994, Santos and Tellería 1994), and none for *J. occidentalis*. Especially lacking are studies of endozoochorous dispersal by frugivorous mammals (but see Chavez-Ramirez and Slack 1993, Muñoz-Reinoso 1993, Schupp et al. 1996). In fact, seed dispersal ecology of temperate frugivorous mammals in general has been all but ignored (Willson 1993).

With the linked objectives of increasing our knowledge of juniper dispersal in particular and seed dispersal by temperate frugivorous mammals in general, we quantitatively describe mammalian endozoochorous seed dispersal of *J. occidentalis* on Juniper Mountain, southeastern Oregon, USA. We discuss results in the context of disperser effectiveness, where effectiveness is the product of the quantity of seed dispersed and the quality of dispersal given each seed; that is, the number of seeds dispersed multiplied by the probability a dispersed seed produces a new adult (Schupp 1993). Although a complete evaluation is premature, our data address aspects of both major components of effectiveness, thus providing a useful framework.

Juniperus occidentalis is a monoecious or dioecious tree found mostly on dry, rocky slopes from 1500 to 3000 m elevation. The 5- to 10-mm diameter fleshy, resinous seed cones mature in their 2nd fall and contain 2–3 seeds, each 2–4 mm long (Adams 1993). At least 12 species of birds feed on *J. occidentalis* cones and disperse seeds; coyotes (*Canis latrans*) are the only frugivorous mammals reported dispersing the seeds (Gabrielson and Jewett 1940, Maser and Gashwiler 1978, R. F. Miller personal communication, L. E. Eddleman personal communication).

Juniper Mountain is a relatively isolated mountain rising to 2036 m along the border of Harney and Lake counties, Oregon, USA (≈42°55′ N, 119°55′ W). Most of the mountain is covered with *J. occidentalis* woodland that is expanding into surrounding sagebrush steppe of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and mixed perennial bunchgrasses. We collected mammal feces at 5

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of 6 permanent plots for a study of *J. occidentalis* physiology and genetics by R. Tausch and R. Nowak. The 2 sites with an eastern aspect are 1600E (1601 m elevation) and 2000E (1994 m); the 3 with a western aspect are 1650W (1653 m), 1800W (1801 m), and 2000W (1987 m). Partial collections were made at 2 other sites: coyote feces at ≈1650 m on the east side (camp) and deer pellets near the summit at ≈2000 m (summit).

We made field collections 22–23 May 1994. Based on the presence of seeds and dried ripe fruits on the ground, we are confident a reasonably abundant cone crop was produced in the season preceding sampling. At each site we spent 1.5–2 h collecting feces of *Sylvilagus nuttallii* (Nuttall's cottontail), *Odocoileus hemionus* (mule deer), *Cervus elaphus* (elk), and *C. latrans* (coyote). We did not use defined plots, but most feces were collected within a 50-m radius; the goal was to quantify frequency of seed occurrence more than density. We slowly walked the area, carefully searching for relatively recent feces. Based on our experience in west central Utah, we believe most feces were from the preceding fall through early spring. For each site we combined all *S. nuttallii* pellets into a single sample and individually bagged ungulate pellet groups and *C. latrans* feces. We returned feces to the laboratory, where they were refrigerated until processing. This involved moistening in plastic bags to soften (5–15 min) before breaking them apart to carefully search for whole juniper seeds and fragments of broken ones.

Seeds were very rare in mammal feces (Table 1), and no patterns were evident across elevation or aspect. On a per site basis, dispersal by *S. nuttallii* was most frequent; seeds were found at 4 of 5 sites, followed by *C. latrans* (3/6), *O. hemionus* (2/6), and *C. elaphus* (0/2). On a per pellet (feces) or pellet group basis, *C. latrans* was the most frequent seed disperser; 13.8% of feces contained seeds. The next highest frequency was an order of magnitude lower; 1.2% of *O. hemionus* pellet groups contained seeds. Similarly, we found 437 seeds in *C. latrans* feces compared to only 8, 6, and 0 in *S. nuttallii*, *O. hemionus*, and *C. elaphus* feces, respectively.

Seeds dispersed by *C. latrans* tended to be deposited with many conspecifics, while seeds dispersed by the other mammals tended to be deposited singly. The 4 *C. latrans* seed-containing feces had 1, 59, 175, and 202 seeds. In contrast, pellets of *S. nuttallii* and *O. hemionus* never contained more than 1 seed, and pellet groups of the latter contained no more than 4 seeds.

Although we have no data on the effects of gut passage on seed viability, most seeds were apparently undamaged—only a single seed in an *S. nuttallii* scat had been broken. Due to the size and hardness of juniper seeds, it is unlikely any were destroyed to the extent they were missed.

Results of this study provide new insight into dispersal of *J. occidentalis* and add support to a growing perception of taxonomic patterns of seed dispersal by north temperate mammals. While rabbits (Smith 1948, Schupp et al. 1996) and deer (Martin et al. 1951) were known to eat fruits and disperse seeds of junipers, the most recent compilation of *J. occidentalis* fruit use (Maser and Gashwiler 1978) lists *C. latrans* as the only mammal dispersing seeds endozoochorously. Although we add *O. hemionus* and *S. nuttallii* to the list, these species disperse very few seeds. With respect to the quantitative component of disperser effectiveness, it appears that only *C. latrans* may be important.

Considering the qualitative component of effectiveness, our data address aspects of both the quality of treatment in the mouth and gut and the quality of deposition (sensu Schupp 1993). The preliminary interpretation is that all species may provide high-quality treatment: virtually all seeds were passed intact without evidence of damage. Very low rates of juniper seed damage by carnivores (Herrera 1989, Chavez-Ramirez and Slack 1993) and lagomorphs (Schupp et al. 1996) have been previously reported and may be a common result. Note, however, that the European rabbit *Oryctolagus cuniculus* feeding on fleshy fruits in Spain (Muñoz-Reinoso 1993) and the Canary Islands (Nogales et al. 1995) breaks seeds and reduces germination of surviving seeds. Carnivores, which often pass seeds with most of the pulp attached, may be less likely to reduce viability and may even increase germination rate (Bustamante et al. 1992).

In contrast, the quality of deposition may be relatively low, especially for *C. latrans*, which deposited large numbers of seeds in individual

TABLE 1. Numbers and frequencies of *Juniperus occidentalis* seeds in defecations of 4 mammal species in southeastern Oregon. See site descriptions in the text. NA = not applicable for that site.

	Collection site							
Species	1600E	1650W	Camp	1800W	2000E	2000W	Summit	Total
Sylvilagus nuttallii								
No. pellets	970	121	NA	228	359	368	NA	2046
No. (prop.) with seeds	1 (.0010)	0 (.0000)	NA	2 (.0088)	2 (.0056)	3 (.0082)	NA	8 (.0039)
No. seeds	1	0	NA	2	2	3[a]	NA	8
Odocoileus hemionus								
No. pellet groups	50	24	NA	40	26	14	16	170
No. (prop.) with seeds	1 (.0200)	0 (.0000)	NA	0 (.0000)	0 (.0000)	1 (.0714)	0 (.0000)	2 (.0118)
No. pellets	5459	2394	NA	4387	2911	1887	2376	19,414
No. (prop.) with seeds	2 (.0004)	0 (.0000)	NA	0 (.0000)	0 (.0000)	4 (.0021)	0 (.0000)	6 (.0003)
No. seeds	2	0	NA	0	0	4	0	6
Cervus elaphus								
No. pellet groups	0	0	NA	0	2	2	NA	4
No. (prop.) with seeds	0 (.0000)	0 (.0000)	NA	0 (.0000)	0 (.0000)	0 (.0000)	NA	0 (.0000)
No. pellets	0	0	NA	0	256	302	NA	558
No. (prop.) with seeds	0 (.0000)	0 (.0000)	NA	0 (.0000)	0 (.0000)	0 (.0000)	NA	0 (.0000)
No. seeds	0	0	NA	0	0	0	NA	0
Canis latrans								
No. scats	6	3	9	3	6	2	NA	29
No. (prop.) with seeds	2 (.3333)	0 (.0000)	1 (.1111)	0 (.0000)	1 (.1667)	0 (.0000)	NA	4 (.1379)
No. seeds	261	0	175	0	1	0	NA	437

[a] Includes 1 broken seed.

defecations. Seed clumping may greatly reduce dispersal success by increasing density-dependent seed predation and competition during establishment (Howe 1989, Chavez-Ramirez and Slack 1993, Schupp 1993). In addition, all species probably deposit few seeds in the most suitable microhabitats. While successful *J. occidentalis* establishment is apparently most likely beneath shrubs (Burkhardt and Tisdale 1976, Miller and Rose 1995), carnivores (Bustamante et al. 1992, Chavez-Ramirez and Slack 1993), lagomorphs (Schupp et al. 1996), and ungulates (E. W. Schupp, J. M. Gómez, and M. Fuentes, unpublished data) tend to defecate and deposit seeds disproportionately often in open interspaces.

Mammals, with the possible exception of *C. latrans*, do not appear to be very effective dispersers of *J. occidentalis*. While these mammals have some role in juniper expansion, it appears to be minor unless rodents harvest seeds from feces and cache them preferentially beneath shrubs. We cannot evaluate the existence and/or importance of such an interaction between phase I and phase II dispersal (sensu Chambers and MacMahon 1994) at this time.

From the perspective of mammalian frugivory in general, our results support Willson's (1993) suggestion that *C. latrans* is one of the most highly frugivorous north temperate mammals and is, along with several other Carnivora, likely to be among the quantitatively most important mammalian dispersers of fleshy-fruited plants in the region. In contrast, lagomorphs and ungulates have been viewed mostly as dispersers of nonfleshy grass and forb seeds consumed incidentally while feeding on foliage (e.g., Welch 1985, Zedler and Black 1992, Malo and Suárez 1995). There is a growing realization, however, that lagomorphs are frugivorous and potentially important dispersers of some fleshy-fruited species (e.g., Smith 1948, D'Antonio 1990, Muñoz-Reinoso 1993, Nogales et al. 1995, Schupp et al. 1996), and that ungulates may occasionally consume large numbers of fleshy fruits, although they may often destroy seeds rather than disperse them (Sargent 1990, Englund 1993).

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TYPE LOCALITY RESTRICTION OF *HYPSIGLENA TORQUATA* GÜNTHER

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Key words: Hypsiglena torquata, *Mexico, Nicaragua.*

Since the description of *Hypsiglena torquata* by Günther in 1860 and the designation of the type locality as Nicaragua, specimens have been collected only in central Mexico and north into the United States (Tanner 1946, Dixon and Dean 1986). Just how far south in Mexico *Hypsiglena* may range is perhaps not yet known. Specimens have been taken in Morelos, Guerrero, and Michoacan but not as yet, to my knowledge, from the states of Mexico, Puebla, Veracruz, Oaxaca, or Chiapas. If *Hypsiglena* occurs in Nicaragua, the question arises as to why additional specimens have not been taken from the intervening areas.

There is now general agreement that *Hypsiglena* does not occur south of Mexico, and perhaps not in southern Mexico; however, Smith and Taylor (1945) list it as "perhaps to Ecuador and Venezuela." Peters (1956) discusses in detail the specimens responsible for placing *Hypsiglena* in South America and concludes that this genus does not occur south of Costa Rica. Peters and Orejas-Miranda (1970) list the distribution of *H. torquata* as "Southwestern United States through Mexico and Baja California to Costa Rica." Savage and Villa (1986) do not include it in their Herpetofauna of Costa Rica, and Villa et al. (1988) do not list it in their Middle American Herpetology. Peters and Orejas-Miranda (1970) list it only to Costa Rica, without including additional records; Savage and Villa (1986) and Villa et al. (1988) exclude *Hypsiglena* from areas south of Mexico. Dunn (1936:6) lists a specimen from Costa Rica (Museo Nacional) but provides no museum number.

Dixon (1965) recognized that there was a problem in accepting Nicaragua as the type locality for *Hypsiglena torquata* Günther. This he based on the similar color pattern of the type when compared with specimens from Mazatlań, Sinaloa. He communicated his concern with Mr. J. C. Battersby at the British Museum, who provided basic character information for the type specimen. Dixon then concluded that "the locality from which the type specimen came is somewhat in doubt" and that "until both co-types are examined and further collecting done, it would be unwise to change the type locality, even though it appears to be in error."

The original description of *Leptodeira torquata* Günther 1860 provides not only an adequate description based on scale patterns but also includes a drawing of the type specimen (Fig. 1A). The drawing exhibits a color pattern that is similar to most specimens seen from south central Mexico and is apparently representative of *H. torquata* from that area (Figs. 1B, C, D). The ventral-caudal counts of 174-174-46-50 listed in the original description total 220–224 for the two type specimens. This does not match the totals for specimens of *H. t. torquata* listed from west central Mexico (Dixon and Dean 1986). A series of 27 specimens that I have examined from Guanajuato, Guerrero, Morelos, Michoacan, Jalisco, and Colina have a ventral-caudal range of 202–214. If the ventral-caudal counts for the types are correct as listed in the original description, it would be difficult to include them in the populations of *H. t. torquata* of central and southwestern Mexico.

To verify the accuracy of the published data for the type, I contacted Dr. Colin McCarthy at the British Natural History Museum for additional information concerning collecting documentation and the accuracy of the scale counts published by Günther (1860). The following response was received:

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[1] M. L. Bean Life Science Museum, Brigham Young University, Provo, UT 84602.

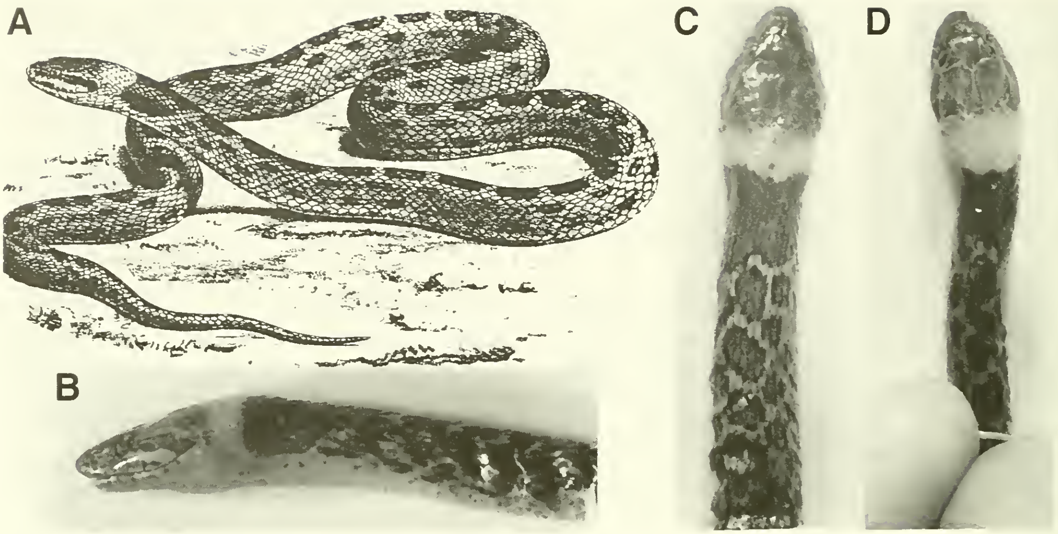

Fig. 1. *Hypsiglena torquata*. A, Drawing of *Leptodeira torquata*, as figured by Günther (1860). B, C, D, Photos of specimens of *H. t. torquata* taken in west central Mexico: B and C, LACM 7269, 58.4 miles SE of Escuinapa, Nayarit; D, BYU 23787, 25 miles S of El Salado, Sinaloa, Mexico.

> I am afraid that there is no additional documentary evidence here regarding the collectors of the specimens. I note that we received it from the Derby Museum, so I imagine that if there was ever any associated documentation of that sort it might be there. The Derby Museum is still in existence though without any names or reference numbers I would have thought it would be impossible for them to provide information.

Dr. McCarthy provided the following data for the type specimen, 46.1.1.15 (formerly 61.12.30.97 as published by Smith and Taylor 1945): "ventrals 170 (Dowling count, add 2 if you prefer to count from the first expanded scale). Subcaudals 42 pairs (+1 terminal scale). It appears to be a female."

In counting ventrals I have always started with the first scale that is noticeably wider than long. It appears that there are in the type 2 questionable scales that Dowling considered gulars; they might be small ventrals. In counting caudals I have always included the terminal scale in the count. Based on the present data, ventrals of the type are either 170 or 172 and caudals 43. These add to 213 or 215 ventral-caudals for the type specimen in the British Museum, which is within the range for females in populations of central or southwestern Mexico.

The present information is not sufficient to place the type locality at a given location, but it does provide sufficient data to place the area of origin in central Mexico. The scale and color patterns could place it in one of the states listed above or perhaps in one of several adjoining states.

Other scale patterns of the type specimen taken from the original description are similar to specimens from central and western Mexico. Quoting Günther (1860): "The medial lower labial is triangular and rather small; nine lower labials, the first of which is in contact with its fellow behind the median shield." One specimen (Taylor 5561, a female) from a series of 8 specimens from Morelos has nearly all scale pattern characteristics of the type specimen: ventrals 171, pre- and post-oculars 2-2, infralabials 9-9, temporals 1-2. The only difference is that the type has 8-8 supralabials rather than 7-7 as in the Taylor specimen. However, other specimens from Morelos have 8-8 supralabials. A specimen (USNM 46513 female) from Michoacan has 173 ventrals, 39 caudals (total 212), and 9–10 infralabials. Other specimens from west central Mexico also approach the scale pattern of the type based on the recount of ventrals and caudals of the type.

By carefully examining the drawing of the type (Fig. 1A), one can see that the artist appears to have virtually duplicated the color pattern of the entire snake. The head, nape, and body pattern are near duplicates of some specimens from Mexico. The white band is about 4 scales in length and the dark nape band 6 or 7. In the series from Morelos, the white band is 4–5 scales long and the dark one 5–6 long. Dorsal body spots range from 45 to 52. In the drawing of the type, I count 43, and there are some hidden by the head. If this is, and it appears to be, an essentially accurate drawing of the type, it seemingly places it with the *Hypsiglena* from west central Mexico.

The color patterns are helpful in placing the type in any of the listed Mexican states, but it is the scale patterns such as the ventral-caudal totals and the infralabials that effectively relate the type to west central Mexico, perhaps to either Morelos or Michoacan.

In the original description 2 specimens were available to Günther. I asked Dr. McCarthy if he knew the location of the 2nd specimen. He referred me to Mr. Malcom Largen at the Liverpool Museum. The following, a rather detailed account of not only the record of the type specimen but also documentary information concerning both type specimens, is his complete statement:

> Dear Dr. Tanner
>
> I regret to report that no example of *Hypsiglena torquata* survives in the Liverpool Museum and that we have no record of when and how the second type specimen was lost. The good news is that I have managed to unearth more than might have been expected about the early history of the type material.
>
> The crucial lead came from our copy of *Ann. Mag. Nat. Hist.* for 1860, in which I found that p. 171 had been contemporaneously annotated with the accession numbers of the type specimens! One of these, 5.8.58.26, appears in the main Stockbook of the "Liverpool Free Public Museum" as "Snake from the Isld. of Laguna, presented by J.O.W. Fabert, 5 August 1858" (see photocopy 1). This same specimen is entered in another register (photocopy 2), where it is identified as "Leptodira torquata, one of the two original specimens described by Dr. Günther." The name was subsequently crossed out because "given in exchange to Dr. Günther for Brit. Museum for a specimen of Xenodon viridis, Dec. 1861." So the type now in London is evidently the one from Laguna Island.
>
> The second specimen, 28.5.53.1, appears in a third, earlier Stockbook of what was briefly called the "Derby Museum." Here (photocopy 3) it is listed as "Snake, found **in a cargo of timber ex nicaragua**, presented by Mr. Roberts, **Duke's Dock (Liverpool)**, 28 May 1853." A later entry identifies this snake as one of "the original specimens described by Dr. Günther under the name Leptodeira torquata. . . ." This is the type that is now lost.
>
> Where is Laguna Island? Evidently, neither Günther (1860) nor any of his contemporaries at Liverpool wrote anything to suggest that they thought it was in Nicaragua. On the contrary, Günther clearly states that his material was believed to originate from two quite separate places and modern citations of the type locality as "Laguna Island, Nicaragua" seem totally unjustified. In short, I suspect that you have good reason to worry about the provenance of these specimens, because I can find no very compelling evidence that *either* snake came from Nicaragua!!
>
> Malcom Largen, Curator of
> Amphibians and Reptiles

All data and the information from England seemed to confirm my conclusion that the types of *H. torquata* Günther had apparently come from Morelos, Mexico. I sent a rough draft of the manuscript to Dr. Hobart M. Smith for his perusal and for any comments he might provide. His response is as follows:

> Isla Laguna makes no sense as a locality, but there is a "Lagunillas" in Morelos not too far from Mexico City, well within the range of the species and in the area you have concluded most likely includes the geographic source of the lectotype.
>
> It is reasonably possible that Lagunillas is the type locality. A label so written could easily be misread as Laguna isla, hence Laguna Isla.

With the present data available and the information provided by Dr. Colin McCarthy, Mr. Malcom Largen, and Dr. Hobart Smith, there is overwhelming evidence to place the type locality of *Hypsiglena torquata torquata* Günther in, at, or near Lagunillas, Morelos, and to designate the available type specimen, British Museum No. 46.1.1.15, as the lectotype for *Hypsiglena torquata* Günther.

I am indebted to many for help and information leading to the conclusions that have been reached in this study. The information provided by Drs. Colin McCarthy and Hobart Smith and by Mr. Malcom Largent made it possible to establish a reasonable, if not the actual, solution to the problem of type locality. (Photocopies of materials from Mr. Largent are available on request.)

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ELEVATIONAL RECORDS FOR MAMMALS IN THE WHITE MOUNTAINS OF CALIFORNIA

Keith Geluso[1], Candace S. O'Connor[1], Sean G. Sullivan[2], and Jack P. Hayes[1]

Key words: high altitude, Lemmiscus curtatus, Mustela erminea, Perognathus parvus, Peromyscus truei.

The White Mountains of California and Nevada lie in the rain shadow of the Sierra Nevada and are very arid. This aridity leads to vegetational zones in the White Mountains occurring at higher elevations than are usual when compared to other mountain ranges in North America (Bole 1938). Consequently, many mammals are found at particularly high elevations (Dunmire 1961, Carey and Wehausen 1991). For example, the chisel-toothed kangaroo rat (*Dipodomys microps*), which typically lives between 1070 and 2130 m, was caught at 3170 m in the Whites (Bole 1938).

During the summers and autumns of 1985–1987 and 1995–1996, we trapped mammals near the Barcroft Laboratory of the White Mountain Research Station. Our trapping resulted in the establishment of 4 high-elevational records for mammals.

We captured 1 piñon mouse (*Peromyscus truei*) at 3660 m, 1 at 3710 m, 1 at 3780 m, and 1 at 4330 m. The previous elevational record was at 3350 m on Mt. Charleston in southern Nevada (Burt 1934), where the mouse was caught among bristlecone pines (*Pinus longaeva*). We trapped 3 of the mice in an alpine fell-field intermixed with large boulder piles. We trapped the 4th mouse 15 m below the summit of White Mountain Peak among rocks on a steep, unconsolidated talus slope. Vegetation near our 3 lower capture sites was mostly dwarf sage (*Artemisia arbuscula*), wax currant (*Ribes cereum*), small forbs, and grasses; vegetation near the summit was exceedingly sparse. The nearest trees were several kilometers from our capture sites.

A male Great Basin pocket mouse (*Perognathus parvus*) was captured at 3690 m in an alpine fell-field. The previous elevational record was at 3048 m on Mount Grant in Nevada (Hall 1946), where 4 individuals were caught on sagebrush-covered slopes on the southwest side of the mountain. Vegetation near our capture site consisted of small forbs and grasses. No sagebrush or trees were present in the surrounding area.

We also caught 2 sagebrush voles (*Lemmiscus curtatus*), 1 at 3930 m and the other at 4270 m. The lower individual was captured in an alpine fell-field, the other on a talus slope with sparse vegetation near White Mountain Peak. Our lowest capture is 490 m higher than the previous record (Dunmire 1961). Dunmire's specimen also was caught in the White Mountains about 10 km from our record. *L. curtatus* is commonly associated with sagebrush, but both our specimens were captured among mixed alpine forbs and grasses.

One ermine (*Mustela erminea*) was captured at 3810 m along a rock outcrop within an alpine fell-field. This capture represents the 2nd highest published record in North America and the highest in the White Mountains. The highest North American capture of *M. erminea* was at 3960 m in Colorado (Armstrong 1972). However, in southern areas of the former Soviet Union this boreal species ranges up to 4000 m (Novikov 1962).

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REPRODUCTION IN THE WESTERN SHOVELNOSE SNAKE, *CHIONACTIS OCCIPITALIS* (COLUBRIDAE), FROM CALIFORNIA

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Key words: reproduction, Chionactis occipitalis, *western shovelnose snake, California.*

The western shovelnose snake (*Chionactis occipitalis*) occurs from southwestern Nevada to the upper end of the Gulf of California, México, and southern Arizona to the desert base of peninsular ranges of southern California (Stebbins 1985). Anecdotal accounts of reproduction in this species appear in Cowles (1941), Wright and Wright (1957), Stebbins (1954, 1985), and Behler and King (1979). In this report I provide information on reproduction of *C. occipitalis* from California.

I examined 135 *Chionactis occipitalis* (109 males, mean snout-vent length [SVL] = 243.1 mm ± 20.2 *s*, range 194–288 mm; 26 females, mean SVL = 267.8 mm ± 23.5 *s*, range 198–308 mm) from California in the herpetology collections of Arizona State University (ASU), Tempe; Museum of Vertebrate Zoology, University of California at Berkeley (MVZ); and the Natural History Museum of Los Angeles County (LACM), Los Angeles (Appendix 1). Counts were made of oviductal eggs or enlarged follicles (>3 mm diameter). The left gonad and part of the male kidney were removed for histological examination, embedded in paraffin, and cut into 5 μm sections. Slides were stained by Harris' hematoxylin followed by eosin counterstain. Testes slides were examined to determine the stage of the male cycle; ovary slides were examined for the presence of yolk deposition. Kidney sexual segments were examined for secretory activity. Histology slides are deposited in LACM.

Data on the male *Chionactis occipitalis* seasonal testicular cycle are presented in Table 1. Testicular histology was similar to that reported in Goldberg and Parker (1975) for 2 other colubrid snakes, *Masticophis taeniatus* and *Pituophis melanoleucus*. In the regressed testes seminiferous tubules contained spermatogonia and Sertoli cells. In recrudescence there was renewal of spermatogenic cells characterized by spermatogonial divisions; primary and secondary spermatocytes and spermatids may have been present. Metamorphosing spermatids and mature sperm were present in spermiogenesis.

Spermiogenic males were found March through July (Table 1). Epididymides and vasa deferentia of spermiogenic males contained sperm. The smallest spermiogenic male measured 194 mm in SVL. Males with regressed testes first appeared in June, suggesting the testicular cycle was nearing its conclusion. The sexual segment of the kidney was enlarged and contained densely staining secretory granules in spermiogenic males. According to Saint Girons (1982), mating coincides with hypertrophy of the sexual kidney segment. Johnson et al. (1982) reported that elevations of blood testosterone levels coincided with hypertrophy of the renal sexual segment in the cottonmouth (*Agkistrodon piscivorous*). The lack of spermiogenic males and the occurrence of males with regressed testes during August–November likely indicate that *Chionactis occipitalis* does not breed during this period.

Data on the *Chionactis occipitalis* seasonal ovarian cycle are presented in Table 2. Reproductively active females were found May–July. I recorded 6 clutch sizes: 11 May, 3 enlarged follicles (4–5 mm diameter); 18 May, 3 enlarged follicles (5–6 mm diameter); 24 May, 2 oviductal eggs (4–5 mm diameter); 27 May, 2 oviductal eggs (5–6 mm diameter); 2 June, 4 enlarged follicles (3–4 mm diameter); 8 July, 2 enlarged follicles (3–4 mm diameter). The vitellogenic follicles in 1 female from 13 August were

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TABLE 1. Monthly distribution of conditions in seasonal testicular cycle of *Chionactis occipitalis*. Values shown are the numbers of males exhibiting each of the 3 conditions.

Month	*N*	Regressed	Recrudescence	Spermiogenesis
March	4	0	1	3
April	22	0	3	19
May	36	0	0	36
June	27	4	0	23
July	13	5	0	8
August	4	4	0	0
September	2	1	1	0
November	1	1	0	0

TABLE 2. Monthly distribution of conditions in seasonal ovarian cycle of *Chionactis occipitalis*. Values shown are the number of females exhibiting each of the 4 conditions.

Month	*N*	Inactive	Yolk deposition	Enlarged follicles	Oviductal eggs
March	1	1	0	0	0
April	5	5	0	0	0
May	13	9	0	2	2
June	2	1	0	1	0
July	3	2	0	1	0
August	1	0	1[a]	0	0
September	1	1	0	0	0

[a] Vitellogenic follicles were undergoing atresia.

undergoing atresia (degeneration). It is thus unlikely that an egg clutch would have been produced. The smallest reproductively active female (enlarged follicles >5 mm diameter) measured 257 mm in SVL. No evidence of reproductive activity (yolk deposition) was seen in the 19 remaining females.

Information on reproduction in *Chionactis occipitalis* includes reports of clutch sizes (2–4; Klauber 1951, Stebbins 1954, 1985, Wright and Wright 1957, Behler and King 1979); clutches are deposited during summer (Behler and King 1979, Stebbins 1985). Cowles (1941) reported 2 March females containing 6 and 9 enlarged ova. Thus, my clutch sizes (2–4) are within the range of previously reported values. The smallest reproductively active female *C. occipitalis* (257 mm SVL) was smaller than the minimal size (289 mm) reported by Klauber (1951).

Only 6 of 24 (25%) of the female sample (collected April–August) were reproductively active, suggesting only part of the female population breeds each year. Breeding by only part of the female population appears to be widespread in snakes. Seigel and Ford (1987) surveyed proportions of breeding females per year for 85 snake species and found proportions varied from 7% to 70%. I have found only part of the female population to breed each year in other North American desert snakes: *Chilomeniscus cinctus*, *Phyllorhynchus browni*, *P. decurtatus*, *Salvadora hexalepis*, and *Trimorphodon biscutatus* (Goldberg 1995a, 1995b, 1995c, 1996).

Klauber (1931,1951) reported *Chionactis occipitalis* has a seasonal activity pattern in southern California that peaks in May–June, with few snakes observed after the end of June (Klauber 1951). This marked seasonal activity pattern accounts for the scarcity of *C. occipitalis* in herpetology collections from months other than May–June and explains why most of my specimens were from these two months. Nevertheless, it is clear from the high percentages of spermiogenic males in May (36/36, 100%) and June (23/27, 85%) that the peak of *C. occipitalis* mating activity coincides with the time of maximum aboveground activity. Moreover, the appearance of 4 of 27 (15%) regressed males in June, 5 of 13 (38%) in July, and 4 of 4 (100%) in August suggests the mating period of *C. occipitalis* is concluding. A similar pattern of peak reproductive activity coinciding with maximum aboveground activity occurred in *Chilomeniscus cinctus* from Arizona (Goldberg 1995c).

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APPENDIX 1

Specimens examined by county from herpetology collections at Arizona State University (ASU), Natural History Museum of Los Angeles County (LACM), Museum of Vertebrate Zoology (MVZ).

Imperial: LACM 9117-19, 52221, 52246, 63618, 133830. **Inyo:** MVZ 61099. **Kern:** LACM 52219, 123760. **Los Angeles:** LACM 52203. **Riverside:** LACM 22623, 22625, 22629-30, 22641, 22643, 22650, 52227-28, 52291-92, 52294, 52296, 52299-300, 52305, 52311, 52313, 52321, 52328-29, 52334, 52341, 52344, 52353-55, 52358-59, 52361, 52365-66, 52376, 52379, 52383, 52386, 52392-93, 52397, 52403-406, 52417, 52421, 52424-25, 52430, 52432, 52434, 63624, 75275, 75278, 102760, 102763, 102765-66, 102768, 102770, 122099-100. MVZ 65749, 66397-98, 74456, 78004, 147938, 180172, 180179. **San Bernadino:** ASU 1620, 23602. LACM 21620-21, 21623-24, 21627-28, 21636-37, 27704-705, 27708, 52205, 52211, 52216, 52234, 52239, 52241, 52245, 52280-81, 52283, 52286, 102772, 133831. MVZ 49935, 49938, 115916, 193306, 204194, 207931, 214636, 215612. **San Diego:** LACM 2185, 27713, 27715, 27717-18, 27720, 52251-52, 52254, 52257, 52261, 52265, 52267, 52270-72, 52275, 52278, 76292-93, 125991.

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BOOK REVIEW

The Western San Juan Mountains: Their Geology, Ecology, and Human History. Rob Blair, managing editor. University Press of Colorado, Niwot, CO. 1996. 406 pp. $39.95, cloth; $22.95, paper.

The Western San Juan Mountains: Their Geology, Ecology, and Human History is a multiauthored book that explores 4 aspects of the western San Juan region: the physical environment, biological communities, human history, and interesting points along the San Juan Skyway. The San Juan Skyway, a national scenic byway, forms a loop through the western San Juan Mountains of southwestern Colorado from Ridgeway through Dolores, Durango, and Silverton, and then back to its origin. The skyway straddles 2 major physiographic provinces, the Colorado Plateau and the southern Rocky Mountains. It contains a diverse geologic background and encompasses 6 major vegetation zones, from the desertlike shrub-steppe region of the Colorado Plateau to alpine areas on the highest peaks of the San Juan Mountains.

Part I, "Physical Environment along the San Juan Skyway," which is well written and detailed, is divided into several chapters. Chapter 2, "Paleotectonic History," explores plate tectonics and has a detailed map of recent earthquake epicenters in the vicinity. The subsequent chapter analyzes Precambrian strata, which form the highest peaks in the area. In Chapter 4, "Paleozoic History," the author shows that by careful study of the composition of rocks, physical features, and fossils in the region, geologists can (1) determine the environments under which they were formed and (2) build a geologic history of the area. The author contends that many of the strata in this region formed over millions of years from deposits of various shallow seas and adjacent mountain ranges. Chapters 5 and 6 consider Mesozoic and early Cenozoic history and volcanic rocks. The next 2 chapters give a concise overview of the ore deposits, minerals, and energy resources that have drawn people to this area since the discovery of mineral sites by the Spanish in the early 1700s. The last chapter in Part I describes the always variable and sometimes severe weather across the region.

The book's editor, Rob Blair, points out that this book is targeted for the amateur naturalist and historian and maintains that if the authors wrote about complex topics in simple terms, much of what they said would be incomplete. In other words, this book, especially Part I, was not written for the casual reader. I found myself referring to the glossary (which is very comprehensive) many times in the course of reading. Although the text in Part I is concise, many maps and diagrams are difficult to decipher.

Part II, "Biological Communities along the San Juan Skyway," is divided into chapters based on broad ecological plant communities. Although easier to read than Part I, this section is not as detailed. Chapter 10, "Ecological Patterns," discusses physical and biological factors that limit species survival to specific habitats. It also has interesting anecdotes about the area's flora and fauna. Although well written, the book is sometimes inaccurate. In Chapter 10, for example, the authors assert that pika and White-tailed Ptarmigan are the only remaining faunal inhabitants in the area from the ice ages. In fact, many invertebrates have survived as well, including the endangered butterfly, Uncompahgre fritillary (*Boloria acrocnema)*, which is thought to have inhabited vast areas during glacial periods and is now relegated to high mountain glacial habitats. Chapter 11 explores the semiarid foothills and valleys of the region, which include the low-elevation shrub-steppe community, pinion-juniper woodlands, mountain shrub community, and ponderosa pine–oak–Douglas-fir woodlands. Chapter 12 discusses the higher elevation mountain communities from mixed conifer and spruce-fir forests to aspen forests, mountain meadows, and alpine areas. The preceding chapters in Part II are quite short and lack the depth needed to cover these topics in detail. Chapter 13 discusses wetlands and riparian areas as well as threats to these areas from stream channelization and acid mine drainage. A considerable portion of this chapter concerns the Animas, the major river in the area. The authors point out that although many upstream portions of the Animas River have been polluted by acid mine drainage, the stretch near Durango is considered an excellent trout fishery because of dilution from other nonpolluted streams in the area. An important omission here is that the trout in this section of the river are all nonnative varieties introduced into these waters. Also lacking in this book (except in Chapter 13) is a discussion on the effects of past human disturbance, present threats to the biotic system, or conservation measures being initiated in the western San Juans. As an example, wolves and grizzly bears once roamed the area and were forced out by European settlers in the late 1800s and early 1900s. Knowing the impacts people have had and are still having on the ecology of an area is essential to understanding the biotic communities that exist in the region today.

Part III, "Human History along the San Juan Skyway," is engaging and thorough. It begins with a chapter on the Anasazi, who had a long-lasting impact on the area. The author of the chapter, Gary Matlock, maintains that the Anasazi did not mysteriously disappear but migrated south into what is now Arizona and New Mexico. He contends the Pueblo Indians along the Rio Grande and the Hopi in northwestern Arizona are descendants of these ancient people (although Hopi creation myth might dispute this fact). The subsequent chapters describe the arrival and expeditions of the Spanish in the 1700s and a history of the Ute Indians, who mainly used the region for hunting and gathering. The last chapter details the life of the miners who settled this area, drove the Utes out, and then were forced to move on as silver, gold, and other minerals were depleted.

Part IV describes 175 points of interest along the San Juan Skyway, the Durango-to-Silverton Railroad, and the Alpine Loop between Lake City and Silverton. Most sites characterized in this section have geological or mining history significance, but other sites such as hot springs, lakes, and some plant communities are also described. Although the maps in Part I are difficult to interpret, those in Part IV are clear and site locations are easy to find.

Even though I have visited the western San Juans countless times for pleasure and research, I learned much about the area from reading this book. This reference would be a fine addition to any library, but it would be particularly valuable for the reader who has an interest in this region (notably in geology or human history).

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BOOK REVIEW

The Natural History of a Mountain Year: Four Seasons in the Wasatch Range. Claude T. Barnes; foreword by Pamela M. Poulson. University of Utah Press, Salt Lake City, UT. 1996. $16.95 softcover.

Claude Teancum Barnes (1884–1968) was a well-known individual in the early part of this century in Utah. His letterhead of 21 August 1946 describes him as "Attorney and Counselor at Law." However, Davis Bitton (Utah Historical Quarterly 49: 317–339) said of him:

> [H]e was identified as a lawyer, businessman, and naturalist. He might also have been counted as a banker, scientific farmer, and politician. And having written some fourteen books and 118 articles he was certainly one of Utah's most published authors. Of all these labels the one he would have preferred is that of naturalist. For sixty years he observed the birds, mammals, trees and flowers, mountains and canyons, clouds and streams of his native Utah. For Claude Barnes there was beauty all around. And not content to keep his appreciation to himself, he wrote about what he saw. In the tradition of Henry David Thoreau and John Muir and Aldo Leopold he used words not only to describe but also to praise the marvels of nature.

He originally wrote and published this volume as 4 separate essays. Wasatch Summer appeared in December 1956 followed by Wasatch Spring in August 1957, Wasatch Autum in March 1958, and Wasatch Winter in May 1959.

Shortly after the last essay was published, he had printed 50 copies of the 4 seasons bound together and entitled *The Natural History of a Wasatch Year.* Interestingly, the bound book did not follow the chronological presentation but commenced with winter and followed the seasons of the year. Each copy was numbered, signed by the author, and given to a particular person or organization. Each essay, when first published, was dedicated to a person. Wasatch Summer was dedicated to Dorothy B. Jenson and the other three to Louise Atkinson. This new edition is dedicated to the latter.

Louise Atkinson frequently accompanied him on his field trips. He said of her:

> My companion, a real botanist, had not only remarkably discerning eyes, but also the ability to capture and hold almost any insect that attracted our attention, a knack she had retained from bare-foot wading days about the pastures and sloughs of her childhood home near the mouth of the Jordan river.

The colorful, eye-catching book cover, showing one of Barnes' beloved mountains in the springtime, sets off this book. The University of Utah Press and Pamela M. Poulson, of Red Butte Garden and Arboretum, have enhanced Barnes' writings without detracting from or changing any of his text. A map, not found in the original publication, covering the Wasatch Front from Mt. Nebo in the south to Mt. Ben Lomond in the north, locates the major canyons that Barnes refers to so many times in his writings. Dispersed in an attractive manner throughout the book are line drawings of 42 plant parts and 9 birds. He also gave scientific names to the organisms he was describing. Animal names then and now have not changed much, but many plant names have. To assist the reader, a plant synonymy of 45 plants is listed at the end of the book.

Ms. Poulson's 3-page foreword enables the reader to catch the flavor of Barnes' prose. Her reason for the publication is aptly summed up in the following paragraph:

> Probably the best reason for republishing these journals is to remind us of what used to be. Though Mr Barnes had more than we, what we still have now is well worth close observation. Nature divulges its innermost secrets only to them who consistently tread its by-paths, ever alert to hear or see its undisturbed manifestations.

I would recommend this book to all who live along the Wasatch Front and to all others who love the beauties of nature so well described by Barnes so many years ago.

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FRESHWATER SPONGES (PORIFERA: SPONGILLIDAE) OF WESTERN MONTANA

Susan H. Barton[1] and John S. Addis[1,2]

Abstract.—Between May 1992 and April 1996, freshwater sponges (Porifera: Spongillidae) were collected at 24 sites, distributed among 6 sub-major drainage basins in western Montana, to determine the species present. Water samples also were analyzed from 16 of these sites and from 9 sites at which no sponges were detected to characterize sponge habitats chemically. Three species of sponges were identified: *Ephydatia muelleri* (Em), *Eunapius fragilis* (Ef), and *Spongilla lacustris* (Sl). A 4th type of specimen was present at 2 sites but could not be identified because of the absence of gemmules and gemmoscleres. At 46% of the sites containing sponges, more than 1 specimen type was present. Sponges were most commonly found near outlets of lakes, attached to sides or undersides of submerged rocks and logs. They appeared as encrusting (Em, Ef, Sl), lobate (Em), and fingerlike (Sl) growths, varying in color from light tan to green. Dimensions of the spicules varied greatly within each species and expanded previously recorded ranges. No factors limiting sponge distribution were identified, but ranges of conductivity (Em) and of silica (Em, Sl), calcium (Em), and magnesium (Em) concentrations were expanded beyond those reported previously.

Key words: freshwater sponges, Porifera, Spongillidae, Ephydatia muelleri, Eunapius fragilis, Spongilla lacustris, *Montana.*

Although freshwater sponges form part of the benthic community in many of the world's lentic and lotic habitats, they are among the least understood of animal groups. Basic questions about their biogeography and ecology remain unanswered (Frost 1991). Their distributions have not been completely determined, and their habitat requirements have not been fully defined.

Freshwater sponges in the United States have been studied most extensively in the East and Midwest. Species present in these regions have been described and their habitats characterized in chemical and physical terms (Old 1932, Jewell 1935, 1939, Poirrier 1969, Harrison 1974). In addition, some attempts have been made to identify factors that affect species distribution (Old 1932, Jewell 1935, 1939, Poirrier 1969, Strekal and McDiffett 1974). Freshwater sponges of the West, in contrast, have received much less attention. This is unfortunate since water quality is an important issue in the western United States and since sponges are potentially valuable bioindicators of water quality (Harrison 1974, Francis and Harrison 1988, Richelle-Maurer et al. 1994).

In the Mountain West only freshwater sponges of Colorado have been studied in detail (Williams 1977, 1980). Freshwater sponges have been collected in Montana (see, for example, Young 1935, Poirrier et al. 1987), but no studies focusing on the freshwater sponges of this state have been published. In this paper we report results of a survey of freshwater sponges in western Montana. The survey was conducted to identify the species present and to determine chemical and physical ranges for each species' habitat. The latter is a necessary step in defining factors that influence sponge distribution.

---

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MATERIALS AND METHODS

Sampling

Between May 1992 and April 1996, we obtained sponge samples from 24 sites in western Montana (listed in Table 1). These sites were distributed among 6 sub-major drainage basins: Missouri-Sun-Smith, Upper Missouri Tributaries, Upper Clark Fork, Lower Clark Fork, Kootenai, and Flathead (Water Quality Bureau 1991). Sites included lakes and ponds, manmade as well as natural, and in some cases the first 50 m of rivers or streams draining lakes and ponds. Most sites were within 2 km of a road.

In most cases we collected samples by wading near the shore and handpicking likely substrata (submerged rocks or logs). Most samples were obtained from substrata submerged at depths of less than 1 m. In 1 lake (Blanchard Lake), samples were collected by diving. Substratum depth in this case was approximately 3 m. We attempted to collect gemmules (asexual propagules) with the samples by scraping the substratum with a knife or gathering a piece of the substratum itself. For transport to the laboratory, samples were placed in small containers with lake water.

Between June and August 1994, surface-water grab samples were taken from 16 sites at

TABLE 1. Surveyed lakes in western Montana containing freshwater sponges.

Lake	County	Locality	Species present[a]
Missouri-Sun-Smith Basin			
Holter Lake	Lewis and Clark	49°59′N/112°00′W	1,3
Upper Holter Lake	Lewis and Clark	46°50′N/112°00′W	1
Upper Missouri Tributaries Basin			
Lower Miner Lake	Beaverhead	45°20′N/113°34′W	1,3
Rock Island Lake	Beaverhead	45°18′N/113°41′W	2,3
Upper Miner Lake	Beaverhead	45°16′N/113°41′W	2
Hebgen Lake	Madison	44°52′N/111°20′W	1,3
Jerome Rock Lake	Madison	45°23′N/111°28′W	2
Pond below Blue Paradise Lake	Madison	44°57′N/111°26′W	2
Quake Lake	Madison	44°50′N/111°26′W	2,3
Willow Creek Reservoir	Madison	45°43′N/111°42′W	1
Upper Clark Fork Basin			
Blanchard Lake	Missoula	47°01′N/113°23′W	2,3,4
Salmon Lake	Missoula	47°06′N/113°24′W	1,2,3
Coopers Lake	Powell	47°05′N/112°55′W	3,4
Pond near West Fork of Bitterroot River	Ravalli	46°06′N/114°11′W	1
Lower Clark Fork Basin			
Diamond Lake	Mineral	47°09′N/115°11′W	1,3
Moore Lake	Mineral	47°11′N/115°15′W	3
Kootenai Basin			
Kilbrennan Lake	Lincoln	48°35′N/115°53′W	1,3
Loon Lake	Lincoln	48°05′N/115°11′W	2,3
Flathead Basin			
Pond near Bailey Lake	Flathead	48°28′N/114°08′W	1
Spoon Lake	Flathead	48°29′N/114°09′W	2
Cedar Lake	Lake	47°40′N/113°57′W	3
Pond below Cedar Lake	Lake	47°40′N/113°56′W	3
Ducharme Lake	Lake	47°37′N/113°57′W	2
Lower Ducharme Lake	Lake	47°37′N/113°57′W	2

[a]Species: 1, *Eunapius fragilis*; 2, *Spongilla lacustris*, 3, *Ephydatia muelleri*; 4, unidentified sponge

the same time sponge specimens were collected. Samples were taken at locations sponges were collected with the exception of Quake Lake, where water and sponge samples were obtained at sites separated by approximately 0.5 km. During this period water samples were also obtained from 9 lakes that lacked sponges. In these cases samples were collected at convenient sites close to shore. Water samples were collected in polyethylene bottles at a water depth of approximately 0.2 m according to the Field Procedure Manual (Water Quality Bureau 1991). Water to be analyzed for total organic carbon (see below) was preserved with H_2SO_4 at a final concentration of 0.2% (v/v).

Identification

We identified sponges on the basis of descriptions provided by Penney and Racek (1968). Appearances and dimensions of spicules and positions of gemmules within the sponge were the principal criteria on which identifications were based.

We isolated spicules from sponge tissue according to methods described in Pennak (1978). Sponge samples were placed in test tubes with nitric acid and boiled. They were allowed to stand for at least 24 h and then were rinsed repeatedly with water and ethyl alcohol before drying and mounting on slides. We did not boil gemmules but allowed them to stand in nitric acid for 1–6 h before rinsing. Two permanent slides, 1 containing intact gemmules and 1 containing megascleres (needlelike spicules of the main sponge skeleton) and microscleres (small, dermal spicules), if present, were made for most specimens collected. Slides were deposited in the invertebrate collection of Carroll College.

Water Analyses

We performed the following analyses on each water sample: methyl orange alkalinity, calcium, total hardness as $CaCO_3$, magnesium, silicon, and total organic carbon. Analyses were performed by the Montana State Chemistry Laboratory following procedures in the U.S. Environmental Protection Agency manuals, Standard Methods for Chemical Analysis of Water and Wastes (1983) and Methods for the Determination of Metals in Environmental Samples (1991), 24–96 h after the water samples were collected. Total hardness as $CaCO_3$ was obtained by multiplying values obtained for calcium and magnesium by 2.50 and 4.12, respectively, and adding the products. Silicon was converted to SiO_2 by multiplying its values by 2.14. Conductivity, pH, and temperature were recorded on site using a Horiba U-10 Water Checker.

RESULTS

From the specimens collected at sites distributed among 6 sub-major drainage basins in western Montana, we identified 3 species of freshwater sponges: *Eunapius fragilis*, *Spongilla lacustris*, and *Ephydatia muelleri*. Locations of sites and types of sponges found at each are indicated in Figure 1 and Table 1. Morphologically distinctive specimens were also obtained at 2 sites located in the Upper Clark Fork Basin, but these could not be positively identified because of the absence of gemmules and gemmoscleres (spicules associated with the gemmule). At 46% of the sites, 2 or more types of sponges were present. Sponge morphologies and habitats are described below.

Eunapius fragilis (Leidy 1851)
Collection Numbers: 1107, 1114, 1120–21, 1128, 1133–35, 1142, 1147, 1164, 1169, 1171
(Figs. 2, 3)

Eunapius fragilis was collected at 10 of the 24 sites. At 4 sites it was the only species collected (Table 1). At the other 6 sites it was collected with *E. muelleri* or with both *E. muelleri* and *S. lacustris.* No sites contained only *E. fragilis* and *S. lacustris.* Most often *E. fragilis* appeared as an encrusting growth on the undersides or sides of submerged logs or, less commonly, rocks. Substrata settled by *E. fragilis* were usually located at the outlets of lakes or ponds. The sponge rarely exceeded 0.5 cm in height, and its color was either tan or green due to the presence of symbiotic algae (Clifford 1991). Conspicuous oscula were usually present (Fig. 2).

Specimens of *E. fragilis* contained megascleres that were sharply pointed at both ends and were smooth and slightly curved. Microscleres are absent in this species. The gemmules, which ranged in diameter from 250

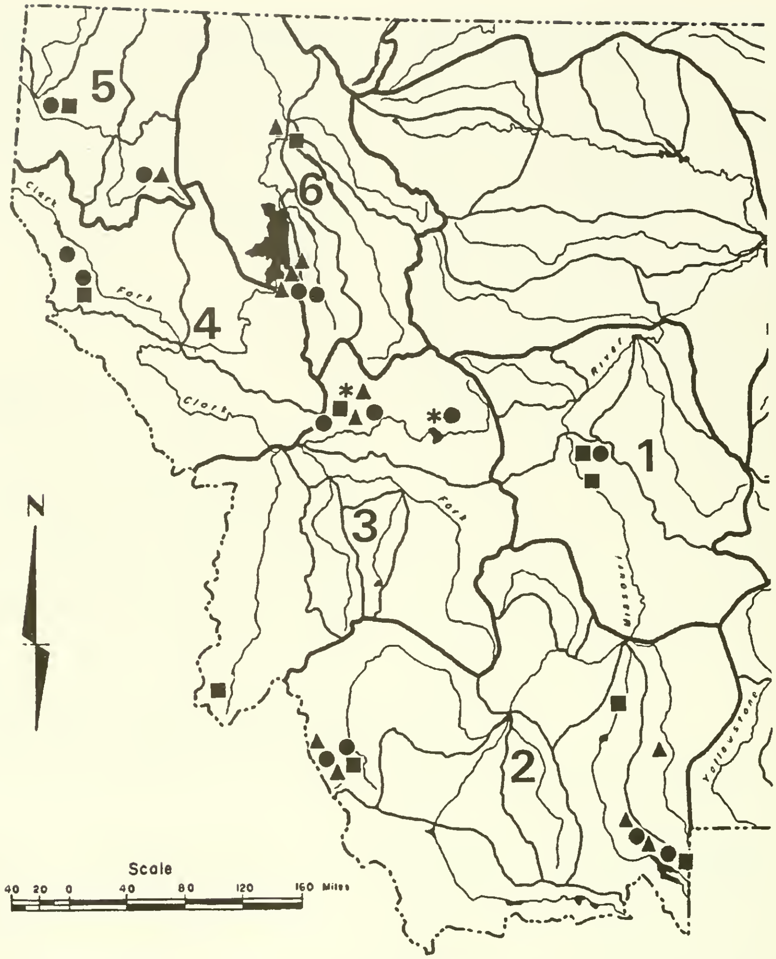

Fig. 1. Distribution of sponge species in western Montana. *Eunapius fragilis*, ■; *Spongilla lacustris*, ▲; *Ephydatia muelleri*, ●; unidentified sponge, ✻. Sub-major drainage basins, outlined by thick lines, are as follows: 1, Missouri-Sun-Smith Basin; 2, Upper Missouri Tributaries Basin; 3, Upper Clark Fork Basin; 4, Lower Clark Fork Basin; 5, Kootenai Basin; 6, Flathead Basin.

to 550 μm, were either arranged in a distinctive pavement layer or clustered in groups of 3–5. Gemmoscleres, oriented tangentially in the pneumatic layer of the gemmule, had blunt, rounded ends, were slightly to strongly curved, and were covered with thick spines, concentrated at the ends. Spicule dimensions are given in Table 2.

One specimen of *E. fragilis* from Diamond Lake, an oligotrophic mountain lake located in the Lower Clark Fork Basin, was unique in that almost every megasclere contained at least 1 expanded bulb along its length (Fig. 3). Normal specimens of *E. fragilis* and *E. muelleri* were also collected from the same region of Diamond Lake.

Spongilla lacustris (Linnaeus 1758)
Collection Numbers: 1099–1100, 1103,
1108–9, 1122, 1124–25, 1132,
1137–38, 1140–41, 1149, 1152, 1154,
1156–57, 1161–63, 1165
(Fig. 4)

Spongilla lacustris was collected at 11 sites. It was the only species collected at 6 sites, and at the 5 other sites it was collected with *E. muelleri* or with *E. muelleri* and either *E. fragilis* or the unidentified sponge (Table 1). More than the other species, *S. lacustris* varied in gross morphology. While often encrusting, it occasionally extended long (>10 cm), cylindrical branches (Fig. 4). It was usually found at

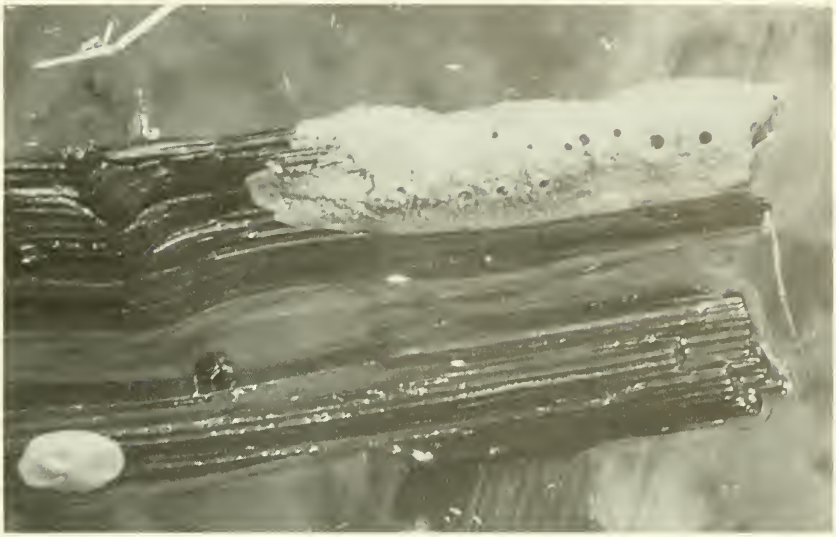

Fig. 2. *Eunapius fragilis* on the underside of a log (pond adjacent to Bailey Lake). Note conspicuous oscula in upper specimen.

TABLE 2. Spicule dimensions of western Montana sponges. Mean ± standard error (range). Dimensions in µm.

	Species		
Spicule dimension[a]	*E. fragilis* (*n* = 13)	*S. lacustris* (*n* = 20)	*E. muelleri* (*n* = 23)
Megascleres			
Length	275 ± 27 (90–392)[a]	287 ± 35 (120–408)[a]	269 ± 19 (150–391)[a]
Width	9.5 ± 1.5 (2.0–14.0)[b]	11.0 ± 2.0 (2.5–19.0)[a]	10.5 ± 1.5 (3.0–18.0)[b]
Microscleres			
Length		67 ± 7 (35–120)	
Width		3.5 ± 0.5 (1.5–7.5)	
Gemmoscleres			
Length	79 ± 13.5 (30–148)[c]	89 ± 24 (25–177)[c]	14.5 ± 1.5 (9.5–25.0)
Width	6.0 ± 1.0 (3.5–8.0)	4.5 ± 1.5 (3.0–9.5)	4.0 ± 0.5 (1.5–7.5)
Rotule diameter			17.5 ± 2.0 (9.5–27.5)

[a] Less and greater than previously reported; see text

[b] Less than previously recorded; see text

[c] Greater than previously recorded; see text

outlets of lakes or ponds, but the branching form of the sponge occurred in quiet water at sites distant from the outlet or at sites near the lake outlet that were not noticeably affected by the current. Usually, *S. lacustris* was found growing on the sides or tops of rocks or logs. The branching form also was found growing directly out of bottom sediments. The sponge was either light tan or green.

Both megascleres and microscleres were sharply pointed at both ends and slightly curved. Megascleres, however, were smooth while microscleres were covered with small spines. Spicule dimensions are given in Table 2.

Gemmules were small, ranging in diameter from 250 to 500 µm, and were typically scattered throughout the sponge. As others have observed (Gilbert and Simpson 1976), gemmoscleres were not consistently present. Those that were found had pointed or rounded ends, were slightly to strongly curved, and were covered with prominent spines.

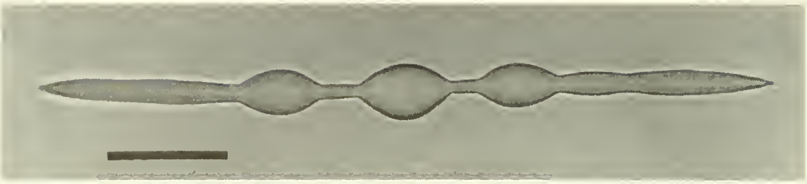

Fig. 3. Abnormal megasclere of *Eunapius fragilis* showing expanded "bulbs" (Diamond Lake). Bar = 50 µm.

Ephydatia muelleri (Lieberkuhn 1855)
Collection Numbers: 1106, 1112–13, 1115, 1118, 1126–27, 1129-30, 1139, 1143-46, 1148, 1150–51, 1158–60, 1167–68, 1170
(Figs. 5–7)

Ephydatia muelleri was collected from 14 sites. At 11 sites it was collected with at least 1 other sponge type (*E. fragilis*, *S. lacustris*, or the unidentified sponge; Table 1). It was found most often on sides or undersides of logs or rocks. The sponge varied in morphology from thin (<0.5 cm) encrustations to lobate forms in which rounded masses (approximately 2 cm tall) extended from basal mats (Fig. 5). Large oscula were sometimes present. Its color varied from light tan to green.

This species, which like *E. fragilis* lacks microscleres, contained megascleres that were sharply pointed at their ends and slightly curved. Although they were often covered with small spines except at their tips, many were smooth or had few spines (Fig. 6). Both smooth and spined megascleres were frequently present in the same specimen. Spicule dimensions are given in Table 2.

Gemmules, ranging in diameter from 350 to 450 µm, were scattered throughout the sponges or were concentrated at the base. A distinct pavement layer was not present, however. The gemmoscleres were birotulate (Fig. 7a). Rotules had similar diameters within each gemmosclere and had irregular and deeply incised rays numbering no more than 12. Shafts connecting the rotules were moderately thick, their lengths usually not exceeding the diameters of the rotules. Gemmoscleres were arranged in a single layer perpendicular to the gemmule and were embedded in a well-developed pneumatic layer.

Slight malformations of gemmoscleres were not uncommon, but those present in sponges from Cedar Lake and an adjoining pond (Flathead Basin) were extreme. Many birotulates had 1 or more spines extending from their shafts, and misshapen rays were often present (Figs. 7b,c).

Unidentified Sponge
Collection Numbers: 1119, 1155, 1172–75
(Fig. 8)

Some specimens collected from undersides of rocks and logs in Blanchard and Coopers lakes lacked gemmules and gemmoscleres and could therefore not be positively identified. Although collected from 2 different sites, these specimens exhibited similar morphologies. At both locations sponges were light tan and formed hard, disc- or cushion-shaped masses. Megascleres were slightly curved, sharply pointed at both ends, and covered with short spines except at their tips. Many megascleres also had a slight midregion expansion (Fig. 8). The megascleres bore an overall resemblance to the spined megascleres of *E. muelleri* but were substantially wider (21.0 ± 1.5 µm versus 10.5 ± 1.5 µm for *E. muelleri*). Normal specimens of *E. muelleri* also were present in both lakes. Specimens collected during return visits to Coopers Lake in November 1995 and February 1996 did not contain gemmules. In fact, specimens of this sponge collected at these times resembled specimens collected during summer months. In contrast, *E. muelleri* had died back and occurred only as mats of gemmules held within skeletal frameworks. The unidentified sponge might be a species of *Ephydatia*, *Trochospongilla*, or *Anheteromeyenia*. Further studies of this sponge are underway.

Chemical and Physical Factors

Chemical and physical ranges characterizing habitats of the identified species are given in Table 3. These ranges were determined from data collected at 16 of the sites that contained sponges. The table also includes ranges

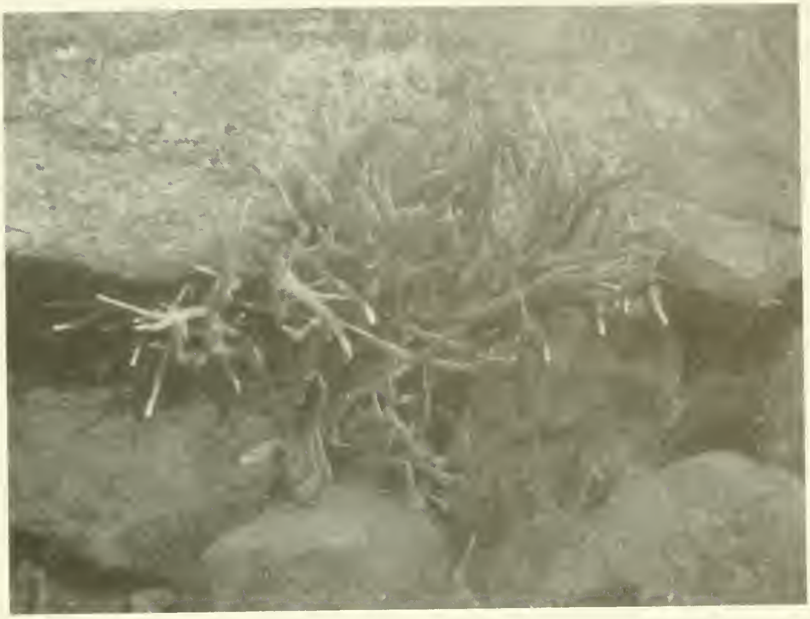

Fig. 4. *Spongilla lacustris* with fingerlike projections growing from beneath a rock (Salmon Lake).

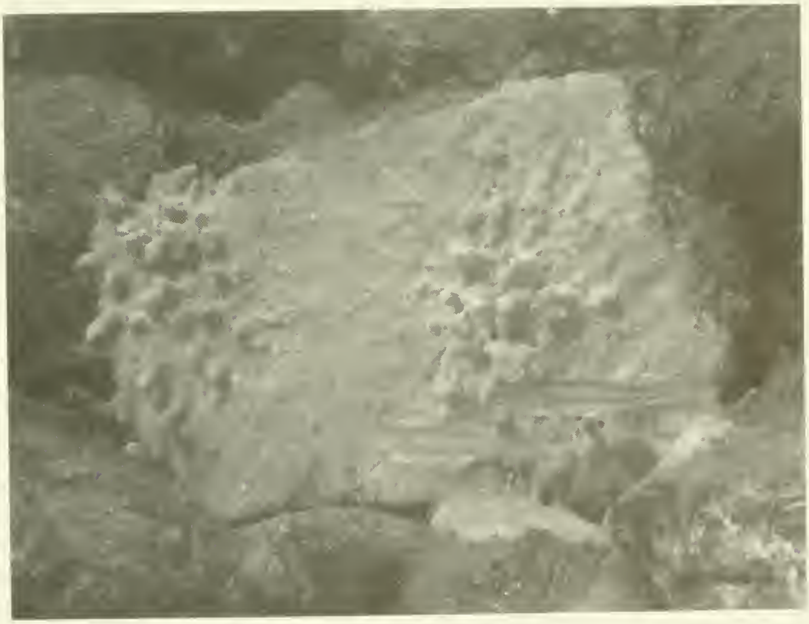

Fig. 5. *Ephydatia muelleri* exhibiting encrusting and lobate growth (Salmon Lake).

derived from data collected at 9 lakes that did not contain sponges. Although there was overlap among the ranges determined for the 3 species, widths of the ranges varied. Chemical ranges determined for *E. fragilis*, except for the ranges of total organic carbon and silica, were wider than those determined for *E. muelleri* or *S. lacustris*. In addition, *S. lacustris* had the narrowest ranges of alkalinity, calcium and magnesium concentrations, and total hardness. Differences between variances of data obtained from sites containing the different

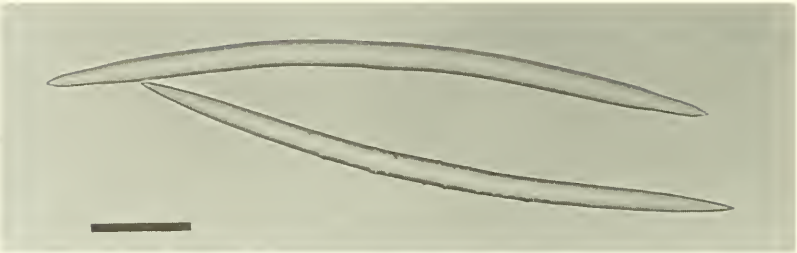

Fig. 6. Smooth and sparsely spined megascleres of *Ephydatia muelleri*. Bar = 50 µm.

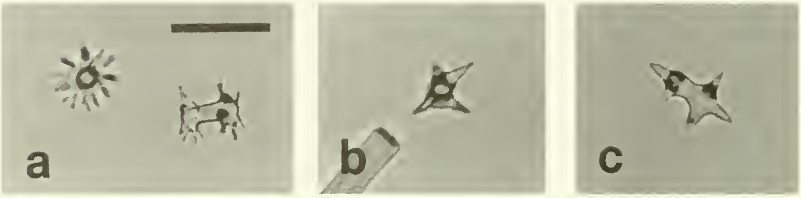

Fig. 7. Gemmoscleres of *Ephydatia muelleri:* a, normal birotulate gemmoscleres, top and side views; b and c, malformed gemmoscleres, top view (b) and side view (c) (Cedar Lake). Bar = 25 µm.

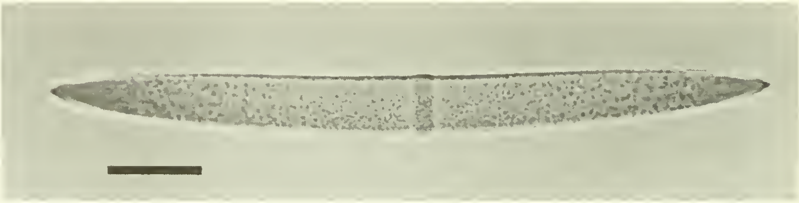

Fig. 8. Megasclere of unidentified sponge (Coopers Lake). Note slight midregion swelling (dark band). Bar = 50 µm.

sponge species, however, were not statistically significant at $\alpha = 0.05$ (Levene's test for equality of variances, one-tailed), although at $\alpha = 0.10$ the variance of the data for magnesium concentration from lakes containing *E. fragilis* was significantly greater than the variance determined from lakes containing *S. lacustris*. Differences among the means of the data were also not statistically significant at $\alpha = 0.05$ (one-way ANOVA).

Some sites that lacked sponges had values for chemical and physical factors that lay outside the ranges determined from sponge-containing lakes, but others had chemical and physical profiles that were very similar to lakes that contained sponges. The difference between means of the data obtained from lakes containing sponges and lakes lacking sponges was not significant at $\alpha = 0.05$ (pooled *t* test).

DISCUSSION

The small number of sponge species found in western Montana is consistent with results of other surveys of sponges of the Mountain West and seems to reflect an overall paucity of sponge species in this region. In his listing of the sponges of Alberta, Clifford (1991) reports only 3 species, the same 3 reported by us: *Ephydatia muelleri, Eunapius fragilis*, and *Spongilla lacustris*. Williams (1980) reports 4 species from Colorado: the previously mentioned 3 plus *Ephydatia fluviatilis*, found at 1 location on the eastern plains. That these 3 species of the 27 reported for the United States and Canada (Frost 1991) were found in western Montana is not surprising when their distributions are considered. All 3 species are widespread. *Eunapius fragilis* is truly cosmopolitan, being present on every continent, whereas *E. muelleri* and

TABLE 3. Chemical and physical ranges of western Montana sponges.

	Lakes containing sponges			Lakes without sponges
Variable	*E. fragilis* ($n = 9$)	*S. lacustris* ($n = 7$)	*E. muelleri* ($n = 10$)	($n = 9$)
Methyl orange alkalinity (mg/L)	11.2–139.0	15.0–80.0	11.2–106.0	0.0–244.0
Calcium (mg/L)	2.0–39.4	4.3–21.4	2.0–30.1[a]	0.4–47.9
Total hardness as $CaCO_3$ (mg/L)	6–151	11–81	6–112	2–231
Total organic carbon (TOC) (mg/L)	0.7–5.1	0.5–6.5	0.0–6.5	0.0–14.4
Magnesium (mg/L)	0.8–12.8	0.0–6.7	0.0–9.0[b]	0.2–27.0
pH	7.06–8.83	7.62–8.39	7.06–8.26	6.11–8.26
SiO_2 (mg/L)	3.2–17.1	2.1–37.9[a]	2.1–37.9[a]	4.9–15.4
Conductivity (µS/cm)	21–355	26–237	38–237[a]	9–420
Elevation (m)	884–2124	1006–2911	884–2537	640–2926
Temperature (°C)	15.8–23.4	13.0–23.4	15.6–23.4	13.0–23.4

[a] Greater than previously recorded, see text

[b] Less than previously recorded; see text

S. lacustris are present throughout the cold-temperate region of the northern hemisphere (Penny and Racek 1968).

Although only 3 species were identified, each showed considerable morphological variation. The variation encompassed spicule size in all 3 identified species, spicule shape in *E. fragilis* and *E. muelleri*, and spine development in *E. muelleri*. Variations of spicule morphology are of concern since taxonomic classification rests largely on this feature.

Spicule size ranges for each species identified were expanded beyond those reported previously (Penny and Racek 1968, Ricciardi and Reiswig 1993). The broader range of megasclere lengths in *E. fragilis* was especially pronounced. Some megascleres observed were >120 µm longer and others were >70 µm shorter than those previously recorded. Short, thin megascleres and long megascleres were sometimes found in the same specimen.

Atypical spicules with bulbs along their lengths were present in 1 specimen of *E. fragilis* collected from Diamond Lake. Simpson and Vaccaro's (1974) report that germanium inhibits silica deposition during spicule formation and can cause spicules with bulbs to form suggests that these malformations might have an environmental basis. Since other specimens of *E. fragilis* in the same area of the lake had normal megascleres, however, the malformations must either be due to highly localized conditions or have a genetic basis. The levels of the measured chemical factors in Diamond Lake were not unusual although values for hardness, calcium, and magnesium were near the upper ends of the ranges we determined from *E. fragilis*–containing sites.

Another type of malformation occurred in gemmoscleres of the specimens of *E. muelleri* collected from Cedar Lake and a nearby pond. Here, gemmoscleres had misshapen rays, and at least 1 spine extended from their shafts. Poirrier (1974) described similar malformations in a related species, *Ephydatia fluviatilis*, and observed that they can be induced by altering environmental conditions, suggesting that the presence of malformed gemmoscleres in Cedar Lake might be due to the environment. Since no chemical or physical data are available for Cedar Lake, we do not know whether unusual conditions exist in this lake.

Finally, smooth megascleres or megascleres having few spines were common in *E. muelleri* throughout western Montana. Both Penny and Racek (1968) in their taxonomic revision of the Spongillidae and Ricciardi and Reiswig (1993) in their description of the sponges of eastern Canada state that *E. muelleri* only rarely has smooth megascleres. Williams (1977), however, reported that in Colorado, *E. muelleri* frequently has smooth megascleres. A high frequency of smooth megascleres therefore might be characteristic of this species in the Mountain West.

Most chemical and physical ranges determined from sponge-containing lakes fell within limits established in previous reports (Jewell 1939, Harrison 1974, Williams 1977). Exceptions were the ranges of conductivity and of calcium, magnesium, and silica concentrations determined for *E. muelleri* and the range of silica concentration for *S. lacustris.*

In her study of Colorado sponges, Williams (1977) observed that broadest chemical ranges were associated with *E. fragilis*, whereas the ranges of alkalinity, calcium and magnesium concentrations, and total hardness determined for *S. lacustris* were significantly narrower than those for *E. fragilis* or *E. muelleri*. Even though the chemical ranges determined for these species were, in several cases, broader in western Montana than in Colorado, similar relationships among the widths of their ranges were observed: *E. fragilis,* in western Montana as in Colorado, had the widest chemical ranges overall (in western Montana, total organic carbon and silica were exceptions), and *S. lacustris* had the narrowest ranges of alkalinity, calcium and magnesium concentrations, and total hardness. From the 2 studies, it appears as if *E. fragilis* in the Mountain West is less constrained by chemical factors than the other 2 species are and that *S. lacustris* is more limited by such factors. These conclusions need to be substantiated by analyses involving larger sample sizes.

The fact that sponges were absent from some lakes having measured chemical and physical profiles almost identical to those of lakes containing sponges suggests that sponge distribution is influenced by more factors than those we examined. In fact, as Williams (1977) pointed out, distribution is probably controlled by chemical, physical, and biological factors acting synergistically. The identification of species of freshwater sponges in western Montana and the initial chemical and physical characterization of their habitats lay the foundation for investigations of the effects of additional factors on sponge distribution.

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BOGGY MEADOWS, LIVESTOCK GRAZING, AND INTERSPECIFIC INTERACTIONS: INFLUENCES ON THE INSULAR DISTRIBUTION OF MONTANE LINCOLN'S SPARROWS (*MELOSPIZA LINCOLNII ALTICOLA*)

Carla Cicero[1]

ABSTRACT.—I surveyed 34 meadows in California and Oregon to count Lincoln's Sparrows (*Melospiza lincolnii alticola*) and to identify habitat features that might influence their local, insular occurrence. Lincoln's Sparrows were found at 72% of the sites surveyed. Counts of singing males were low and uncorrelated with meadow size. Lincoln's Sparrows were most common in wet meadows with little damage by grazing. Singing males were concentrated in flooded or boggy areas near meadow edges, where pines (*Pinus* sp.) provided elevated perches for singing and vigilance. Patches of willows (*Salix* sp.) were often present nearby. Numbers of male Lincoln's Sparrows were strongly and negatively correlated with abundance of sympatric Song Sparrows (*M. melodia fisherella*). Lincoln's Sparrows breeding in montane meadows are potentially vulnerable to local extirpation because of their insular distribution, low population density, and fluctuating habitat conditions. Heavy damage from livestock grazing drastically increases the probability of local extirpation.

Key words: Melospiza lincolnii, *Lincoln's Sparrow, montane meadow, insular populations, habitat association, livestock grazing, conservation biology,* Melospiza melodia, *Song Sparrow.*

Meadows form ecological islands throughout montane forests of the western United States. Although these systems generally support a rich avifauna, they are highly variable in terms of physiographic, hydrologic, edaphic, vegetative, and floristic characteristics (e.g., see Kuramoto and Bliss 1970, Benedict and Major 1982, Ratliff 1982, 1985, Allen 1987). Grazing and fire history also shape meadow environments (Kuramoto and Bliss 1970, DeBenedetti and Parsons 1979, 1984, Parsons 1981, Ratliff 1985). Changes in grazing and fire management practices, combined with climate, further influence the ecology and stability of meadows by promoting invasion of lodgepole pine and other conifers (Franklin et al. 1971, Dunwiddie 1977, Vale 1981a, 1981b, Ratliff 1985).

Because of their mobility, birds respond quickly to habitat change and thus are model organisms for illustrating the effect of habitat on the distribution and abundance of insular as well as continental populations (Cody 1981, Wiens 1989). Numerous researchers have examined total avifaunal distribution and abundance on montane islands (e.g., Johnson 1975, Kratter 1992, Lentz 1993), in natural habitat patches (e.g., aspen; Flack 1976), or in disturbed forest fragments (e.g., Forman et al. 1976). However, detailed studies of *specific* taxa occupying natural insular habitats such as meadows are scarce.

The montane form of Lincoln's Sparrow (*Melospiza lincolnii alticola;* Miller and McCabe 1935, American Ornithologists' Union 1957) is well suited to such a study. This taxon breeds insularly in particular kinds of meadows from Oregon to California and from Idaho to New Mexico. Such sites are separated from other suitable islands of habitat by unoccupied coniferous forest. Two other subspecies (*M. l. lincolnii* and *M. l. gracilis*) occur more broadly in brushy bogs from central Alaska through Canada to the northern contiguous United States. Despite the widespread distribution of Lincoln's Sparrows, the species has been poorly studied compared with either of its congeners, the Song Sparrow (*M. melodia*) or Swamp Sparrow (*M. georgiana*). Information on the distribution and natural history of *M. l. alticola* is especially lacking. In this study I provide baseline data on occurrence, abundance, habitat association, and other factors potentially related to their local distribution in western montane meadows. Secondarily, I evaluate the potential impact livestock grazing has on this taxon.

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Range ecologists have shown unequivocally that grazing occurs unevenly across montane vegetation types and that meadows and other riparian areas receive disproportionately heavy use relative to their total acreage (Cook 1966, Roath and Krueger 1982a, 1982b, Gillen et al. 1984, Platts and Nelson 1985). Numerous studies have assessed the impact of such use on riparian habitats and associated wildlife (e.g., Leege et al. 1981, Kauffman et al. 1983, Kauffman and Krueger 1984, Taylor 1986, Ohmart 1994). Montane Lincoln's Sparrows are potentially vulnerable to disturbance by heavy grazing because of their tendency to nest on or near swampy ground in wet meadows (Grinnell and Miller 1944, Austin 1968). Consequently, changes in their local occurrence or abundance may reveal degradation of meadows by livestock.

STUDY AREAS AND METHODS

I surveyed meadows for Lincoln's Sparrows from mid-May to early July 1987–1989. A total of 34 meadows belonging to 29 systems were visited, including 1 in northern Oregon and 28 in California from the southern Cascade Mountains (Lassen County) through the Sierra Nevada to the San Bernardino Mountains (Fig. 1). Elevations ranged from 1365 to 2470 m, with lodgepole pine (*Pinus contorta*) forest dominating the surrounding vegetation. Size, land ownership, and type and intensity of livestock grazing varied among meadows. Although several

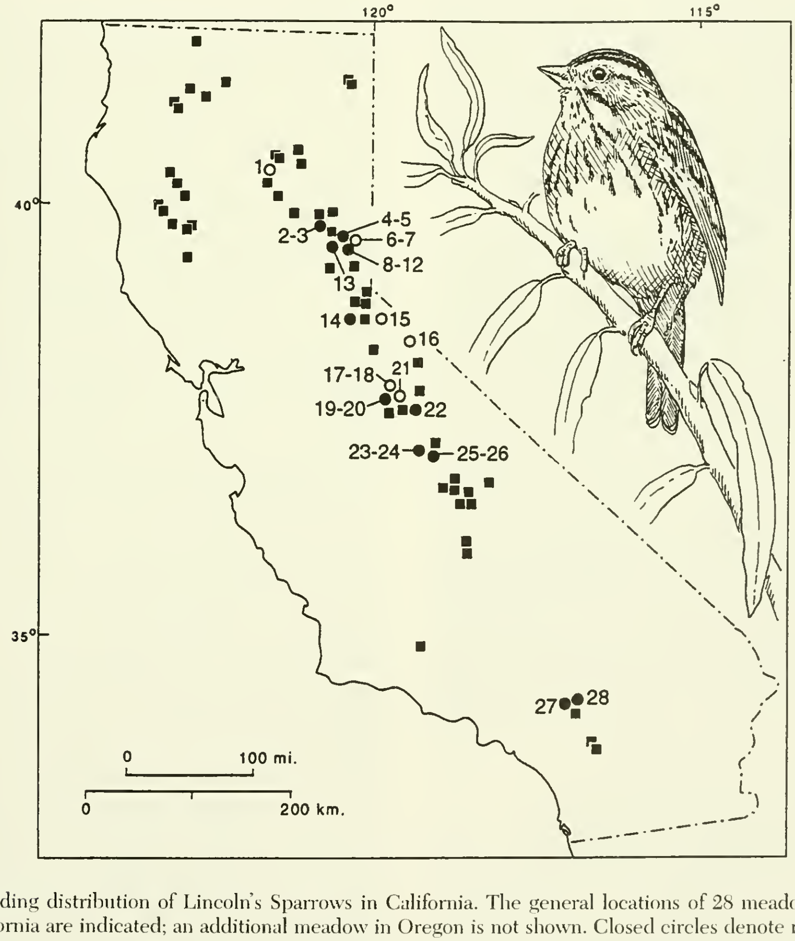


Fig. 1. Breeding distribution of Lincoln's Sparrows in California. The general locations of 28 meadow systems surveyed in California are indicated; an additional meadow in Oregon is not shown. Closed circles denote meadows where Lincoln's Sparrows were present; open circles, meadows where Lincoln's Sparrows were absent. Closed squares show other known breeding localities based on specimens deposited in the Museum of Vertebrate Zoology, Berkeley, California; published records (Grinnell and Miller 1944, Lentz 1993); records obtained during a survey of meadows for Willow Flycatchers (*Empidonax traillii*, M. A. Flett and J. Harris unpublished data).

groups of meadows were clustered geographically, differences in habitat characteristics, elevation, and/or grazing regime occurred between even the most proximal sites. Consequently, each meadow was treated as an independent sample point. Twenty-five sites consisted of single meadows without any connection to other sites. Another meadow (Beasore Meadow [site 22]) was divided by a fence into 2 parts with strikingly different grazing regimes; because the 2 sides also contrasted dramatically in abundance of Lincoln's Sparrows, they were separated for purposes of analysis and discussion. Three meadow systems (Lacey [8], Haypress Creek [9], and Sagehen Creek [12]) contained multiple meadows within 1 drainage or basin that were separated from each other by a distance of at least 0.8 km. Because these were visited only during the breeding season, when males were singing and thus territorial, presumably there was no movement of Lincoln's Sparrows between meadows. This was confirmed by multiple visits to the same meadow system (e.g., Haypress Creek) during a single breeding season, when individual singing males could be identified repeatedly by their location in each meadow.

To ensure breeding status, counts were limited to singing males. Lincoln's Sparrows sing vigorously from elevated perches during the breeding season, particularly near watercourses or along the meadow edge, and thus are easily detectable. Numbers of singing males were counted by traversing each meadow and recording their presence and location. Because my goal was to survey a broad range of sites in order to evaluate the *kinds* of meadows inhabited by montane Lincoln's Sparrows, lengthy and repeated visits to individual meadows were not possible. However, the size and discrete, linear configuration of most meadows enabled complete surveys of *all* singing males during 1 or, at most 2, consecutive mornings (2–5 h/morning). Thus, standard census techniques appropriate for expansive areas of noninsular habitat were unnecessary.

Complete counts of singing males were obtained at 26 (76%) of the 34 meadows. Partial surveys were conducted at the remaining 8 sites because of their large size and/or because fencing restricted access. Nonetheless, these estimates still provide valuable information regarding the occurrence of Lincoln's Sparrows. Six of the 8 sites were visibly impacted by grazing. Surveys took longer in large meadows or at sites with high numbers of Lincoln's Sparrows. Because the amount of time spent at each site varied, count values were standardized by dividing the number of singing males observed per visit by the length of the survey. As with all count methods, some silent males may have been overlooked. Thus, these counts represent minimal estimates of total abundance.

The geographic scope of this study precluded surveying all meadows simultaneously. To verify the reliability of counts conducted at different times, I surveyed 17 meadows (50%) twice or more during the same or subsequent seasons. Counts of singing males in the same meadow at different stages of the breeding cycle were identical. Because annual climatic differences might also influence counts taken in different years, I obtained data on mean temperature and precipitation during May and June 1987–1989 (National Oceanic and Atmospheric Administration 1987, 1988, 1989) from weather stations located near 3 main clusters of meadows: (1) northern Sierra Nevada—Sagehen Creek, Nevada County, California, 1932 m; (2) central southern Sierra Nevada—Huntington Lake, Fresno County, California, 2140 m; (3) San Bernardino Mountains—Big Bear Lake, San Bernardino County, California, 2070 m. I analyzed these data by analysis-of-variance using Statview for the Macintosh (Abacus Concepts 1988). With the exception of mean June temperature, which was slightly different among years ($P = 0.0387$), there was no annual effect on temperature or precipitation ($P > 0.05$). I counted similar numbers of Lincoln's Sparrows at the same meadow in different years.

In a daily field journal, I recorded numbers of other singing birds at each meadow and provided detailed descriptions and sketches of the meadows. I also took notes on the characteristics of meadows with and without Lincoln's Sparrows, and on the location of singing males relative to the meadow edge and to habitat features such as extent of flooding, presence or absence of willows (*Salix* sp.), presence or absence of corn lily (*Veratrum* sp.), and presence or absence of pines (*Pinus* sp.). The first 3 habitat variables (flooding, willows, corn lily) are presumably important for breeding (Grinnell and Miller 1944, Austin 1968, Speirs and Speirs 1968). Although published accounts do not provide information on the use of edges

TABLE 1. Rating scheme used for characterizing meadows based on wetness and extent of grazing damage.

Score	Characterization
WETNESS	
1	Meadow very dry: no standing water or boggy ground; single, well-defined stream channel
2	Less than 25% of meadow wet: few areas of standing water or boggy ground
3	25–50% of meadow wet: some flooded or boggy areas, other areas dry
4	50–75% of meadow wet: many areas of standing water or boggy ground; some rivulets of running water
5	75–100% of meadow wet: most or all of meadow covered with standing water and/or rivulets of running water
GRAZING	
1	Meadow essentially pristine: no bare ground exposed; grassy, undercut streambanks; no evidence of gullying and/or bank erosion; few to no signs of livestock
2	Slight grazing damage: <25% of meadow with bare ground exposed; slight gullying and/or streambank erosion; low density of livestock droppings and trails
3	Moderate grazing damage: 25–50% of meadow with bare ground exposed; gullying and/or streambank erosion clearly evident; low to moderate density of livestock droppings and trails
4	Heavy grazing damage: 50–75% of meadow with bare ground exposed; pronounced gullying and/or streambank erosion; moderate to high density of livestock droppings and trails
5	Meadow severely damaged: >75% of meadow with bare ground exposed; extreme gullying and/or streambank erosion; very high density of livestock droppings and trails

and/or pines, observations of singing males suggest that these features might be equally important. Because of the broad geographic sampling and concomitant variability in meadow type, data on the herbaceous composition of each meadow were beyond the scope of this study. Differences in habitat features associated with individual males ($n = 75$) were tested statistically using a nonparametric binomial test, with the normal approximation for $N > 35$ (see Siegel and Castellan 1988:38–44).

A complex classification system has been developed for meadows in the Sierra Nevada, incorporating similarities in physiographic, hydrologic, edaphic, vegetative, and floristic characteristics (Ratliff 1985). However, only "in a few situations have enough sites been studied to adequately define the [classification] series" (Ratliff 1985:9). Because of the close association between breeding Lincoln's Sparrows and boggy or flooded ground, I used a simpler approach to rate meadows on a scale of 1 to 5 according to wetness (Table 1). Scores assigned to meadows reflect the wetness characteristics observed during the period of study. Higher or lower ratings may be more appropriate at other times depending on seasonal and annual variability in hydrologic regimes.

Quantitative information on livestock use in each meadow was difficult to obtain because of variability in land-ownership patterns and because stocking rates, determined for entire grazing allotments, do not accurately reflect the concentration of livestock on meadows and other riparian areas. Consequently, damage to meadows caused by livestock grazing (see Fig. 2) was assessed subjectively and also rated on a scale of 1 to 5, taking into account the amount of bare ground exposed, extent of gullying and/or streambank erosion, presence of old or recent livestock droppings, and network of livestock trails (Table 1). As with wetness, scores were assigned based on overall damage observed during the period of study. Although gradient and/or soil type also may contribute to differences in erosion seen between meadows, impacts from grazing clearly had a major effect. Evaluation of the effects of grazing on plant species composition and diversity was beyond the scope of this study. Both wetness and grazing damage may vary with changes in grazing practices.

Areas of meadows were estimated from USGS 7.5-minute topographical maps using a point-grid system modified for a scale of 1:24,000; these data were supplemented by U.S. Forest Service data where available. For large meadows where counts are incomplete, both the total area and the area surveyed were estimated.

RESULTS

Distribution and Abundance of Lincoln's Sparrows

I found Lincoln's Sparrows in 26 (76.5%) of the 34 sites surveyed (Table 2). Absolute numbers of breeding males varied from 1 to 16, which translates to standardized counts of 0.2–4 males/h. Counts were low in most meadows:

TABLE 2. Characteristics of meadows surveyed for *M. l. alticola* in California (1–28) and Oregon (29). See Figure 1 for locations in California.

Meadow[a]	Total area (ha)	Area surveyed (ha)	Number of surveys[b]	Time per survey (h)	Number of singing males	Number of singing males per survey hour	Wetness score[c]	Grazing damage score[c]	Type of grazing[d]
1. Battle Creek Meadows, 1460 m (P)	511	447	1	10	0	0.0	3	4	Cattle
2. Grass Lake, 1980 m (NF)	5	5	1	2	3	1.5	5	1	Not grazed
3. Church Meadows, 2040 m (P)	6	6	2	5	11	2.2	3	2	Sheep
4. French Meadows, 2035 m (P)	16	16	1	3	6	2.0	2	3	Cattle
5. Lincoln Valley, 2220 m (P)	26	26	3	4	16	4.0	4	1	Cattle?[e]
6. Cottonwood Creek, 1770 m (NF)	52	52	2	4	0	0.0	4	2	Sheep
7. Perazzo Meadows, 2010 m (P)	369	59	1	5	0	0.0	3	4	Cattle
8A. Lacey Valley, 2070 m (P)	164	120	1	5	1	0.2	2	3	Sheep
8B. Little Lacey Valley, 2085 m (P)	42	42	1	2	3	1.5	3	4	Sheep?[e]
9A. Upper Haypress Creek, 2195 m (NF)	20	20	2	2	4	2.0	4	2	Not grazed
9B. Middle Haypress Creek, 2110 m (NF)	8	8	3	2	3	1.5	3	1	Not grazed
9C. Lower Haypress Creek, 2035 m (NF)	26	26	2	3	2	0.7	2	2	Not grazed
10. Coppins Meadow, 2070 m (P)	164	60	2	4	8	2.0	3	3	Cattle
11. W of Coppins Meadow, 2070 m (P)	9	9	2	2	4	2.0	4	1	Cattle
12A. Upper Sagehen Creek, 2050 m (NF)	14	14	2	3	2	0.7	2	2	Sheep
12B. Lower Sagehen Creek, 2010 m (NF)	54	54	2	4	1	0.3	4	1	Not grazed
13. Austin Meadow, 2070 m (NF)	6	6	1	3	2	0.7	2	3	Cattle
14. Leek Spring Valley, 2255 m (P)	56	49	1	2	4	2.0	3	2	Cattle?[e]
15. Pleasant Valley, 1850 m (P)	207	51	1	2	0	0.0	1	4	Cattle
16. Swauger Canyon, 2390 m (NF)	?[f]	23	1	2	0	0.0	4	1	Sheep

<2 males/h were recorded in 16 (61.5%) of the 26 meadows, 2–3 males/h in 8 meadows, and 3–4 males/h in only 2 meadows. Numbers of singing males were highest at Church Meadows (3) and Lincoln Valley (5) in the northern Sierra Nevada, Bluff Lake (27) and Metcalf Creek (28) in the San Bernardino Mountains, and Hood River Meadows (29) in northern Oregon. Counts were not correlated with meadow size ($r = 0.240$, $P > 0.05$).

Distribution and abundance were clearly associated with scores for wetness and/or extent of grazing damage (Fig. 3). Lincoln's Sparrows were most common in moderately wet to very wet, i.e., flooded, meadows with low levels of grazing damage. Except for Little Lacey Valley (8B) and Upper Beasore Meadow (22A), the species was absent from all meadows with heavy grazing pressure (score $\geq$ 4). The presence of Lincoln's Sparrows at these 2 sites is accounted for by the method of analysis, in which scores were assigned based on overall appearance of the meadow. Thus, all 3 males at Little Lacey Valley were concentrated in the lower, wetter portion of the meadow, where impacts from grazing were slight; none was observed in the more heavily damaged, upper reaches. Likewise, the single male in Upper Beasore Meadow occurred at the lower edge of the site, which was in good condition relative to the meadow as a whole. As expected, Lincoln's Sparrows were absent from the single site that lacked standing water and showed signs of heavy grazing (Pleasant Valley [15]).

TABLE 2. Continued.

Meadow[a]	Total area (ha)	Area surveyed (ha)	Number of surveys[b]	Time per survey (h)	Number of singing males	Number of singing males per survey hour	Wetness score[c]	Grazing damage score[c]	Type of grazing[d]
17. White Wolf, 2380 m (NP)	6	6	1	2	0	0.0	3	1	Not grazed
18. Ackerson Meadow, 1400 m (P)	139	61	1	3	0	0.0	2	4	Cattle
19. Hogdon Meadow, 1400 m (NP)	30	30	1	4	3	0.8	4	2	Not grazed
20. Crane Flat, 1890 m (NP)	22	22	1	3	2	0.7	3	1	Not grazed
21. Porcupine Flat, 2470 m (NP)	6	6	1	2	0	0.0	2	1	Not grazed
22A. Upper Beasore Meadow, 2088 m (P)	16	16	2	3	1	0.3	2	5	Cattle
22B. Lower Beasore Meadow, 2057 m (P)	15	15	2	3	5	1.7	3	2	Not grazed?[e]
23. Poison Meadow, 1740 m (NF)	10	10	2	2	2	1.0	3	2	Cattle
24. Markwood Meadow, 1800 m (NF)	45	45	1	3	4	1.3	4	3	Cattle
25. Dinkey Meadow, 1680 m (P)	37	37	2	4	6	1.5	4	2	Cattle
26. Long Meadow, 2100 m (NF)	15	15	2	4	3	0.8	3	3	Cattle
27. Bluff Lake, 2315 m (NF)	7	7	2	3	8	2.7	3	1	Not grazed
28. Metcalf Creek, 2225 m (NF)	7	7	2	4	11	2.8	4	1	Not grazed
29. Hood River Meadows, 1365 m (NF)	12	12	1	3	11	3.7	5	1	Not grazed

[a] Multiple meadows within a single system are designated alphanumerically. Letters in parentheses indicate dominant ownership (P = private; NF = national forest; NP = Yosemite National Park). Specific localities and dates of surveys are available from the author.

[b] Surveys were conducted on 1–2 consecutive days. This was sufficient to count every singing male in all of the areas surveyed (see Methods).

[c] Rated on a scale of 1 to 5 (see Table 1).

[d] Determined from fieldwork and U.S. Forest Service data. Applies only to this study period; ungrazed meadows may have been grazed in prior years.

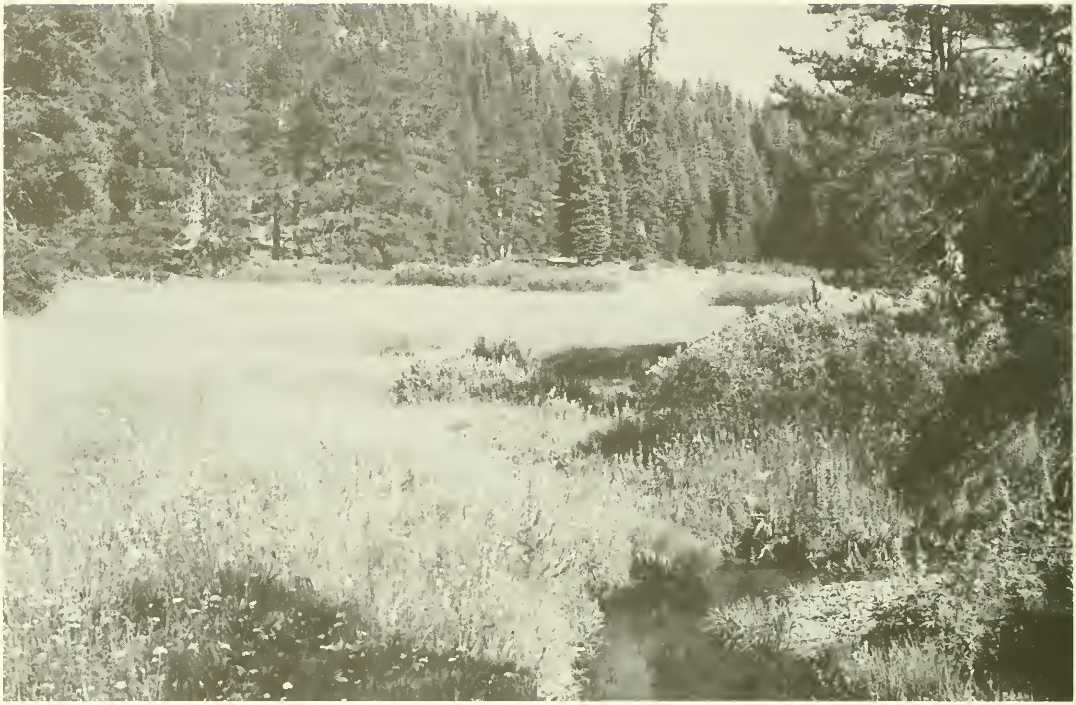
[e] Data unclear. In Lincoln Valley I found no evidence of recent grazing, although the Tahoe National Forest lists this meadow as part of the Lincoln Valley allotment. Information was not available for Little Lacey Valley, Leek Springs Valley, or Lower Beasore Meadow. Little Lacey Valley was obviously grazed, presumably by sheep because of sheep grazing in adjacent Lacey Valley. Leek Springs Valley did not appear to have recent grazing activity, although the general area has numerous grazing allotments and this meadow probably receives some impact from cattle. Lower Beasore Meadow also did not appear to be grazed, in contrast to the heavily grazed Upper Beasore Meadow (see Fig. 2).

[f] Not estimated because numerous small, patchy openings occur along the canyon bottom.

Despite this general tendency, the distribution of Lincoln's Sparrows showed a more complex pattern. For example, I failed to find the species in several meadows with fairly high scores for wetness and low scores for grazing damage (Cottonwood Creek [6], Swauger Canyon [16], White Wolf [17]). Although abundance was highest in the wettest, most pristine meadows (e.g., Lincoln Valley [5], Metcalf Creek [28], Hood River Meadows [29]), other equally wet sites had notably fewer males (e.g., Upper Haypress Creek [9A], west of Coppins Meadow [11], Lower Sagehen Creek [12B], Hogdon Meadow [19], Markwood Meadow [24], Dinkey Meadow [25]). Meadows with lower wetness scores also supported relatively high numbers of Lincoln's Sparrows as long as grazing damage was fairly low (e.g., Church Meadows [3], Coppins Meadow [10], Bluff Lake [27]).

Habitat Features Associated with Individual Male Lincoln's Sparrows

Singing males were strongly associated with particular habitat features (Fig. 4). The most important attribute was the presence of nearby surface water. Only 3% of the males were observed in areas of dry ground, while 93% were seen in either boggy (54.2%) or flooded (38.9%) sites (a difference significant at $P < 0.001$). Numerous locations had networks of small, narrow channels with runing water that coursed through tussocks of sedges, grasses, or other herbaceous plants. The presence of willows, corn lily, and pines (especially *P. contorta*) also appeared to be important attributes of Lincoln's Sparrow habitat. Approximately 84% of all males occurred near clumps of willows ($P < 0.001$), and 59% were in areas with at least scattered



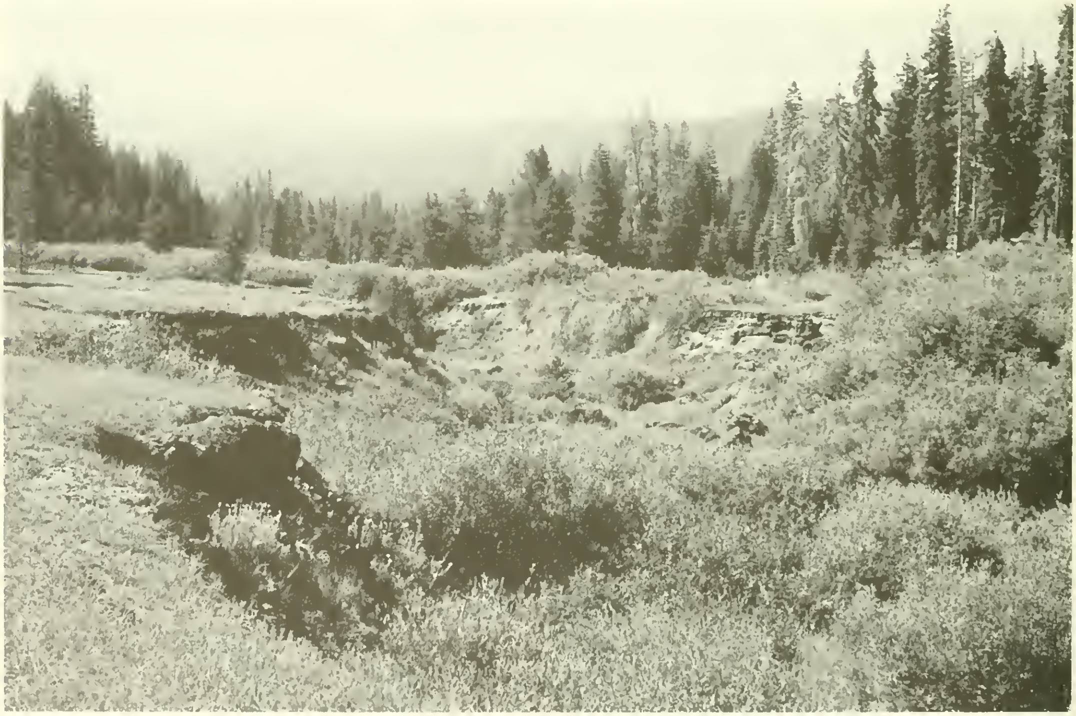


Fig. 2. Views of the lower (top) and upper (bottom) portions of Beasore Meadow, Madera County, California (site 22). Photos illustrate 2 extremes in the condition of meadows surveyed in this study. Lower Beasore Meadow, which was not grazed, had an uneroded creekbank, swampy ground, rich herbaceous cover, and scattered patches of willow (*Salix* sp.). Upper Beasore Meadow showed severe soil erosion, compaction, and dessication due to cattle grazing, with 3–7 m gullying. Lincoln's Sparrows were fairly common in Lower Beasore Meadow but essentially absent from Upper Beasore Meadow. Song Sparrows were abundant in the willows in Upper Beasore Meadow.

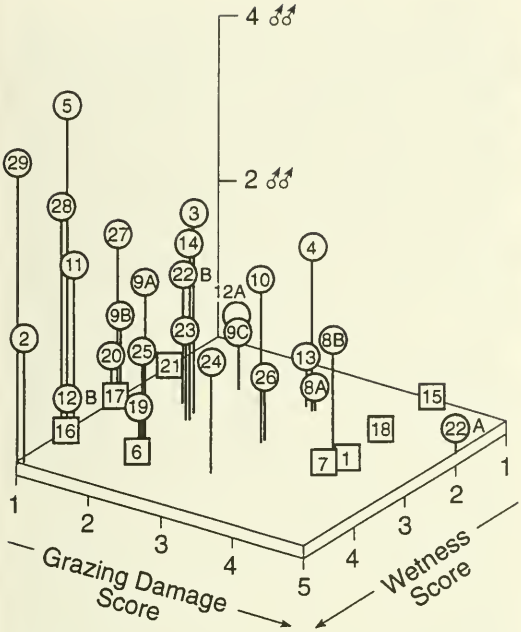


Fig. 3. Three-dimensional graph illustrating the relative abundance (vertical axis; counts per hour) of singing male Lincoln's Sparrows in 29 meadows systems scored according to wetness and grazing damage (see Table 1). Meadows are numbered as in Table 2. Circles indicate sites with Lincoln's Sparrows; squares, sites where Lincoln's Sparrows were absent.

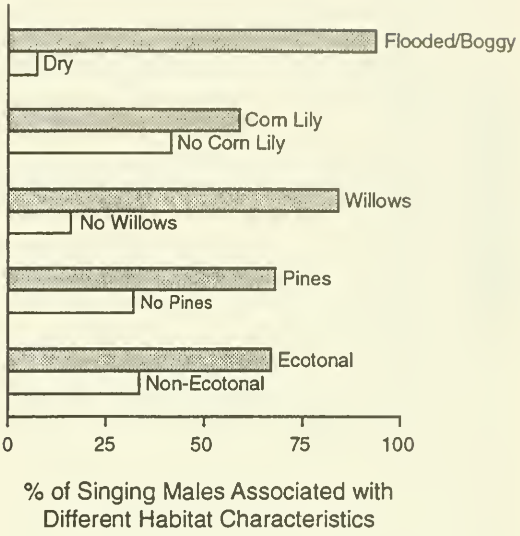


Fig. 4. Proportion of singing male Lincoln's Sparrows associated with different habitat attributes. Ecotonal males were those singing along the edge between the meadow and adjacent coniferous forest. All pairwise comparisons, except for the presence/absence of corn lily, were significant at $P < 0.01$.

patches of lily (although this proportion was nonsignificant, $P = 0.0823$). However, unlike Song Sparrows, which were observed only in areas with willow, Lincoln's Sparrows were not limited to willow patches. The concentration of male Lincoln's Sparrows was greatest near the edges of meadows (67% of males, $P < 0.01$), where they were often seen perched or singing in pines (68% of males, $P < 0.01$). Although most Lincoln's Sparrows were observed within meadows, singing males or pairs were occasionally seen in small, nearby openings in surrounding forest as long as suitable habitat was present.

Data from egg sets at the Western Foundation of Vertebrate Zoology (WFVZ) also revealed the importance of wet ground and clumps of herbaceous vegetation or shrubs for breeding. Of 65 records from California, 56 contained information on moisture characteristics at the nest site, and 54 (96%) of these indicated damp to very wet conditions. Over 90% of the nests were placed on the ground or slightly aboveground, where they were well concealed by tufts of grass and/or other plants. Approximately 35% of the nests in the WFVZ records were situated under a patch of willows.

Negative Association Between Distribution and Abundance of Lincoln's Sparrows and Song Sparrows

Counts of singing male Lincoln's Sparrows and Song Sparrows showed a strong negative correlation ($r = 0.701$, $P < 0.01$; Fig. 5). Although some meadows had approximately equal numbers of the 2 congeners (e.g., Dinkey Meadow, Little Lacey Valley, Lower Beasore Meadow), most sites appeared to be dominated by one or the other species. Song Sparrows were common at several meadows where Lincoln's Sparrows were either absent (Battle Creek Meadows, Cottonwood Creek, Perazzo Meadows, Pleasant Valley, Swauger Canyon, and Ackerson Meadow) or rare (Lacey Valley, Sagehen Creek, Upper Beasore Meadow). These sites included dry, heavily grazed meadows as well as wet, fairly pristine areas that otherwise looked suitable. Likewise, Song Sparrows were absent or rare from several meadows with relatively large numbers of Lincoln's Sparrows (e.g., Lincoln Valley, Coppins Meadow, Metcalf Creek, Hood River Meadows), as well as from

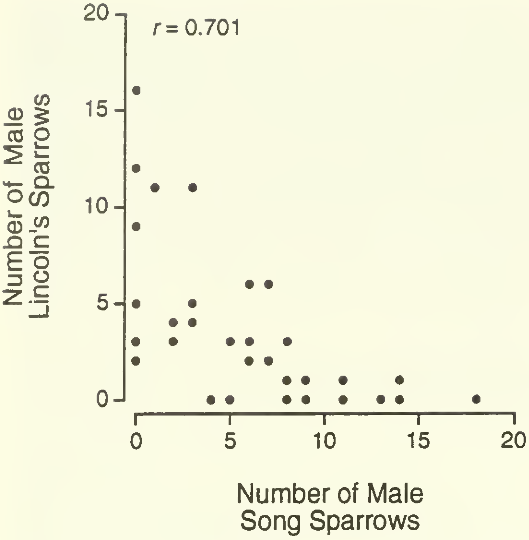


Fig. 5. Negative correlation between number of singing male Lincoln's Sparrows and Song Sparrows.

other sites where Lincoln's Sparrows were less common (west of Coppins Meadow, Austin Meadow, Leek Spring Valley).

The negative association between these 2 species was also evident when comparing counts between meadows within a single system. For example, whereas Lincoln's Sparrows outnumbered Song Sparrows at Upper Haypress Creek (4 versus 2 males, respectively), Song Sparrows were slightly more numerous than Lincoln's Sparrows at Middle Haypress Creek (6 versus 3 males), and noticeably more abundant at Lower Haypress Creek (8 versus 2 males). Similar patterns were observed within single sites. Although approximately equal numbers (3 males) of the 2 species were observed at Little Lacey Valley, for example, Lincoln's Sparrows occurred in the wettest portion of the meadow while Song Sparrows were found only in the drier, more heavily grazed areas. Similarly, although both Lincoln's Sparrows and Song Sparrows were fairly common in Lower Beasore Meadow (5 and 3 males, respectively), the former species dropped out in Upper Beasore Meadow, while Song Sparrows increased significantly in abundance to 14 males.

DISCUSSION AND CONCLUSIONS

Of the 34 meadows surveyed, Lincoln's Sparrows occurred only in sites with certain habitat features. Data on the specific locations of singing males, combined with descriptions of nest sites from WFVZ egg data slips, indicate that combinations of the following attributes are important for breeding: boggy or flooded ground; thick groundcover of herbaceous vegetation, often with raised tussocks of live or dead grasses or sedges; patches of corn lily; willow thickets or other low shrubs; and some conifers. Raised clumps of herbaceous vegetation are probably critical for breeding under such wet conditions, as suggested by the nest site descriptions. Likewise, dense herbaceous plant material, in conjunction with willows and corn lily, may provide important concealment. The association between male Lincoln's Sparrows and pines undoubtedly reflects the importance of elevated perches for singing and vigilance.

Although Lincoln's Sparrows were present in the majority of wet meadows studied, their absence at certain sites that otherwise looked suitable deserves discussion. One example is White Wolf (17) in Yosemite National Park, where Beedy and Granholm (1985:190) reported the species in summer but did not present any dates of nesting. Although Grinnell and Storer (1924:471) noted that Lincoln's Sparrows arrive in the Yosemite region by mid-May, this date may apply to lower elevation meadows in Yosemite Valley. White Wolf is one of the highest (2380 m) meadows surveyed in this study, and it is possible that the timing of my visit in early June preceded the arrival of this species for breeding. However, examination of museum records (MVZ, WFVZ) showed that Lincoln's Sparrows already have nests with eggs by early to mid-June at sites of similar or higher elevation, both in the central Sierra Nevada and elsewhere. Furthermore, I observed Lincoln's Sparrows singing in mid-May at other high-elevation meadows such as Bluff Lake and Metcalf Creek, when temperatures were cold and snow was still present on the ground. Although these 2 meadows were visited in a different year than White Wolf, the lack of a significant annual difference in climate during the period of study suggests that timing alone cannot account for the disparity. Additional surveys are needed to determine the population status of Lincoln's Sparrows breeding at White Wolf.

Another wet meadow where I failed to find Lincoln's Sparrows was Swauger Canyon (16), northeast of Yosemite National Park in the

Sweetwater Mountains. According to Johnson (1975), the species has never been found to nest in that range despite extensive fieldwork there by parties from the Museum of Vertebrate Zoology. More puzzling was the absence of Lincoln's Sparrows along Cottonwood Creek (6) and Lower Sagehen Creek (12B) in the northern Sierra Nevada, especially since the species breeds regularly at other comparable meadows in the same region. (Subsequent visits to these 2 sites have confirmed the results of earlier counts.) Both meadows had large areas that were flooded by beaver (*Castor canadensis*) activity during the period of study. Unlike Lower Sagehen Creek, however, the meadow along Cottonwood Creek is grazed by sheep during the summer, with the season of use occurring from mid-June through September (S. F. Bishop personal communication). Although damage caused by sheep (e.g., trampling of herbaceous vegetation, browsing of willows) may be sufficient to disrupt breeding of Lincoln's Sparrows along Cottonwood Creek, it does not explain their rarity along Lower Sagehen Creek.

In contrast to Lincoln's Sparrows, Song Sparrows were among the most common birds seen at both of these meadows, with abundance higher than at most other sites surveyed. Differences in habitat choice and tolerance for disturbance may account, at least partially, for the unexpected negative association between the 2 species at these and other meadows surveyed. For example, Song Sparrows were abundant at several dry, severely grazed sites that were unsuitable for Lincoln's Sparrows. Likewise, heavily flooded areas such as Hood River Meadows may be shunned by Song Sparrows (only 1 singing male was observed). Of greater interest than these extremes, however, are the patterns observed at intermediate sites, which were often dominated by one or the other species. In fact, Lincoln's Sparrows were common at a number of wet meadows that appeared similar in habitat to both Cottonwood Creek and Lower Sagehen Creek and where Song Sparrows were surprisingly scarce. One hypothesis is interspecific competition, acting in concert with differences in habitat use and/or tolerance for disturbance caused by grazing. Speirs and Speirs (1968:1440) noted that Song Sparrows often utilized the same perches and were able to "compete strongly and very successfully" against Lincoln's Sparrows. I observed interspecific interactions on at least 5 occasions and, in all cases, Song Sparrows instigated the chase, displacing male Lincoln's Sparrows singing from elevated posts. Although there is no evidence that Lincoln's Sparrows and Song Sparrows are interspecifically territorial, additional behavioral and ecological studies are needed to understand the underlying factor(s) responsible for the negative association observed between these 2 congeners on both a local and regional scale. Removal experiments, in which Song Sparrows are excluded from boggy meadows within the range of Lincoln's Sparrows, would especially shed light on the role of interspecific competition, if any, in controlling Lincoln's Sparrow distribution and/or abundance.

Spatial or temporal fluctuations in the distribution and abundance of certain bird species may indicate short-term or long-term trends in climate, resource availability, and habitat quality. Such effects are probably most pronounced in populations occupying ecological islands, which may be in nonequilibrium dynamics (Johnson 1975, 1995). Species with narrow habitat requirements are especially useful as indicators of trends because of their greater vulnerability to natural or human-induced changes. Of the 4 species of sparrows occupying meadows in the Sierra Nevada–Cascade mountains (Savannah Sparrow [*Passerculus sandwichensis*], Song Sparrow, Lincoln's Sparrow, and White-crowned Sparrow [*Zonotrichia leucophrys*]), Lincoln's Sparrows may be most susceptible to local extirpation because of their generally low population size and their restriction to wet or flooded areas. Although different lines of evidence suggest that mountain meadows may be as temporally stable as the surrounding environment (Benedict 1982), moisture characteristics of meadows are highly variable depending on annual precipitation. Short-term fluctuations in precipitation may affect habitat quality directly through snowmelt and groundwater recharge (Wood 1975) and/or indirectly through availability of food (e.g., insect) resources (Cody 1981, Johnson 1995). In addition, beaver activity can profoundly influence the extent of flooding in meadows.

Livestock grazing can alter natural hydrologic regimes by increasing runoff and exacerbating erosion and gullying, thereby lowering the groundwater table (e.g., Upper Beasore Meadow, Fig. 2B; also see Rauzi and Hanson 1966, Lusby 1970, Platts 1981, Kauffman et al. 1983, Ratliff 1985). Consequently, grazing may eliminate potential nesting habitat for Lincoln's Sparrows. In addition, hydrologic and vegetative changes associated with grazing can alter the distribution and abundance of more tolerant species such as Song Sparrows, which may compete with Lincoln's Sparrows for territories and other resources. These indirect effects of livestock grazing, combined with direct impacts such as reduction of cover and trampling of nests, undoubtedly have resulted in the extirpation of Lincoln's Sparrows from some meadows. Because populations of this species are already vulnerable to natural fluctuations in moisture, any further changes caused by grazing may exacerbate their probability of local extirpation.

Careful range management practices can significantly reduce the impacts of grazing on plant and animal communities in riparian or meadow ecosystems (Leege et al. 1981, Gillen et al. 1985, Taylor 1986, Schulz and Leininger 1990, Popolizio et al. 1994, Bich et al. 1995). Although range condition will vary with landownership patterns (Loring and Workman 1987), strict control of grazing intensity and season of use will result in higher abundances of breeding birds, primarily through increased shrub volume and height (Taylor 1986). Long-term exclusion of livestock on meadows, combined with erosion-control measures, will especially benefit Lincoln's Sparrows and other similar species because of the combined vegetative and hydrologic effects. Baseline data on abundance and distribution, such as those provided in this study, are essential for monitoring population trends resulting from disturbance or restoration of sensitive, ephemeral meadow systems.

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DENSITY, DISTRIBUTION, AND HABITAT OF FLAMMULATED OWLS IN IDAHO

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ABSTRACT.—From 1990 to 1992 we surveyed for Flammulated Owls (*Otus flammeolus*) in 3 areas in Idaho: Salmon National Forest (SNF), Payette National Forest and adjacent Hells Canyon National Recreation Area (PNF-HCNRA), and Nez Perce National Forest (NPNF). We also collected and summarized information on all historic and modern records of Flammulated Owls in Idaho. Flammulated Owls were detected on 65% of 68 routes (2–16 km in length) surveyed at densities ranging from 0.04 to 1.25 singing males/40 ha. Owls were detected on survey routes as early as 10 May and as late as 23 July. Mean percent canopy cover estimated at owl locations on the PNF-HCNRA and NPNF study sites ranged from 52% to 64%, while shrub cover ranged from 16% to 21% and ground cover was 39% to 49%. Our surveys and summary of distributional records indicate that Flammulated Owls occur throughout the montane forests of Idaho in old or mature stands of open ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and stands co-dominated by those 2 species. Fire suppression and timber harvest activity in ponderosa pine forests represent 2 main threats to the species' future security in Idaho. More research on the effects of various silvicultural treatments on Flammulated Owl populations is warranted.

Key words: Flammulated Owl, Otus flammeolus, *population densities, distribution, broadcast tape recordings, habitat, Idaho, ponderosa pine,* Pinus ponderosa, *Douglas-fir,* Pseudotsuga menziesii.

The Flammulated Owl (*Otus flammeolus*) is a small, insectivorous owl that nests in montane forests of western North America and apparently migrates to the Neotropics (McCallum 1994a). On its breeding grounds it is primarily associated with forests containing yellow pine, either ponderosa pine (*Pinus ponderosa*) or Jeffrey pine (*P. jeffreyi*; Reynolds and Linkhart 1992).

Knowledge of the biology of the Flammulated Owl comes principally from studies conducted in Colorado (e.g., Reynolds and Linkhart 1987a, 1987b), New Mexico (McCallum and Gehlback 1988, McCallum et al. 1995), Oregon (Goggans 1986), and British Columbia (Howie and Ritcey 1987). Although the Flammulated Owl has been documented as a nesting species in Idaho (Burleigh 1972, Hayward 1986, Hayward and Garton 1988), little published information exists on its breeding status, distribution, habitats, or population density (Stephens and Sturts 1991).

We conducted surveys for Flammulated Owls from 1990 to 1992 at 3 study sites: (1) Salmon River mountains on the Salmon National Forest in east central Idaho (Atkinson and Atkinson 1990), (2) several small mountain ranges located primarily on the Payette National Forest in west central Idaho (Moore and Frederick 1991), and (3) Salmon River and Clearwater mountains on the Nez Perce National Forest in north central Idaho (Shepherd and Servheen 1992). Herein we report the distributions, densities, and habitats used by Flammulated Owls in these areas and summarize the statewide distribution based on a compilation of historic and modern records of Flammulated Owls in Idaho.

STUDY AREA AND METHODS

We surveyed for Flammulated Owls on portions of the Salmon National Forest (SNF), Lemhi County (45°15′N, 114°15′W), in 1990; the Payette National Forest (44°45′N, 116°30′W) and adjacent Hells Canyon National Recreation Area (45°35′N, 116°25′W) in Adams, Washington, and Idaho counties (PNF-HCNRA) in 1991; and the Nez Perce National Forest

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(NPNF), Idaho County (45°40′N, 115°50′W), in 1992 (Fig. 1).

Survey routes 2–16 km in length were placed in areas containing large stands of mature ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*). We broadcasted taped recordings or vocal imitations of territorial songs for owls along trails or roads from dusk until 0200 h at stations established 500 m apart on the SNF and PNF-HCNRA sites and 500–800 m apart on the NPNF study site. Distances between broadcast stations were based on the distance that we determined singing owls could be heard on our study sites. Howie and Ritcey (1987) estimated that Flammulated Owls are usually heard within 0.5 km under most weather and habitat conditions. At each broadcast station we listened for 1–2 min for unsolicited male songs, then alternated 1-min broadcasts of the songs with 1- to 2-min listening intervals for a total of 10 min. We estimated the azimuth and distance for each owl heard and recorded time and weather on each survey route. On the SNF and PNF-HCNRA study sites (1990–91), we surveyed each route only once, while on the NPNF study site (1992), each route was surveyed 2–3 times. Surveys were conducted 11 May–10 July on the NPNF, 10 May–23 July on the SNF, and 22 May–11 July on the PNF-HCNRA.

Broadcast stations were mapped on 1:24,000 or 1:62,000 USGS topographic maps and 1:24,000 or 1:15,840 orthophotos. In 1990 (SNF study site only) we estimated the densities of responding owls on each linear survey route with the soundscape formula modified from Howie and Ritcey (1987):

$$\text{Area (ha)} = 100\,[n\pi r^2 - (n - 1)\,.2985]$$

where n equals the number of stops per route and r equals the maximum distance at which owls can be heard, a distance assumed to be 0.5 km (Howie and Ritcey 1987). This formula assumes that surveys are conducted along linear transects, a correct assumption for the SNF study site. Because we used roads and trails for survey routes on the PNF-HCNRA and NPNF study sites that did not conform to linear transects, we measured survey areas on these study sites with a planimeter to estimate the density of responding owls for each survey route. All areas within 500 m of broadcast stations were used in density calculations. These 2 techniques for estimating density have the same assumptions and are mathematically comparable.

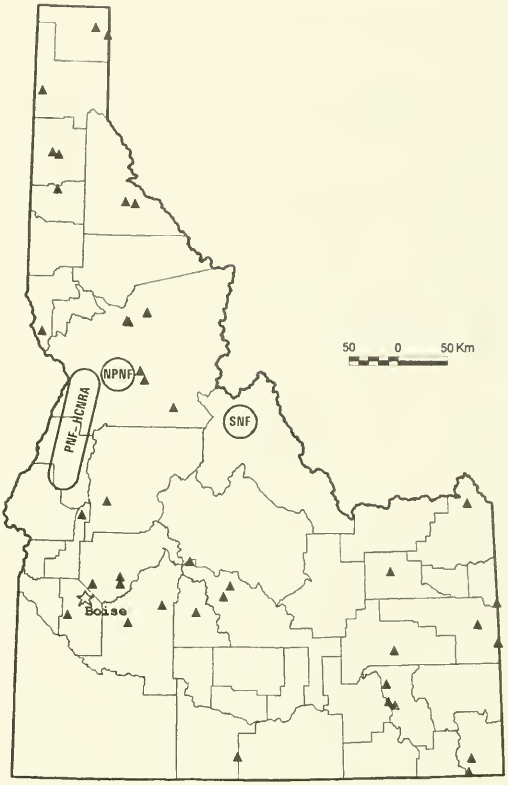

Fig. 1. Location of the Salmon National Forest (SNF), Payette National Forest–Hells Canyon National Recreation Area (PNF-HCNRA), and Nez Perce National Forest (NPNF) study sites. Triangles represent records for Flammulated Owls in Idaho located outside of these 3 study sites (see Appendix A).

On the PNF-HCNRA and NPNF study sites, we characterized the stand-level habitat at owl locations by measuring habitat characteristics following methods described in Noon (1981) on five 0.04-ha circular plots, 1 plot centered on the estimated or known owl location and the other 4 located 50 m from the center plot in the 4 cardinal directions. To minimize the effects of error in estimating azimuth and distance in the habitat analysis, we used only those owl detections estimated to be within 200 m of broadcast stations. Additionally, we used only those owl locations that we did not think were influenced by broadcasting tapes because the owl called before we began broadcasting (13 locations) or the owl began calling immediately after the broadcast and had likely not yet moved in response to the taped call (4 locations).

Tree density and diameter-at-breast-height (dbh) were measured on each plot with the point-center quarter method (Cottam and Curtis 1956). Other measurements collected on each plot included elevation, topographic position, aspect, dominant tree cover and understory vegetation, number of canopy layers (ocular estimate), past silvicultural treatment, stand age, percent canopy cover (densiometer), percent ground cover (line intercept), percent shrub cover (line intercept), and distance to nearest snag with cavity (Moore and Frederick 1991). Stand age was defined as follows: (1) immature—trees not cone bearing, (2) mature—trees cone bearing, and (3) old—multiple canopy layers, abundant large snags, trees with dbh >64 cm (from Noon 1981). Data from the five 0.04-ha plots were combined to calculate means for canopy cover, ground cover, shrub cover, tree density, and dbh.

At the PNF-HCNRA study site, we also investigated **macrohabitat** characteristics through an analysis of the type of habitat, age of forest, and type of timber harvest that occurred in 400-m radius (50.3-ha) circles (approximately the diameter of a Flammulated Owl territory [Reynolds and Linkhart 1987a]) centered on the owl's estimated location. We overlaid these 50.3-ha circles on 1:15,840 aerial photos and 1:24,000 orthophotos on which Forest Service silviculturists had delineated polygons and assigned them to the following classes based on air photo interpretation and stand exams (Moore and Frederick 1991): nonforest (canopy closure <10%), clearcuts (seedlings not visible on photo), open woodlands (noncommercial forests with low canopy closure, poor accessibility, and poor regeneration), selective cuts, immature (poles and saplings visible on photo, trees generally <50 yr old), mature (trees 50–100 yr old), old (trees >120 yr old), and other (water, unclassified lands). The area of these classes within each 50.3-ha circular plot was estimated with a planimeter.

In addition to the surveys conducted in this study, we collected information on all historic and modern observations or records of Flammulated Owls in Idaho. We examined the collection records of all natural history museums in Idaho (College of Idaho, Boise State University, University of Idaho, Idaho State University), records from American Birds, records from the state's primary ornithological treatment (Burleigh 1972), records from a database developed by Stephens and Sturts (1991) for publication of their latilong bird book, and records from the Idaho Conservation Data Center (Idaho Department of Fish and Game), a comprehensive database on the status and distribution of Idaho's rare, threatened, and endangered flora and fauna. Appendix A provides a summary of these records and observations.

RESULTS

Owl Densities and Distribution

From 1990 to 1992 we conducted 85 surveys on 68 survey routes distributed over 3 national forests (Table 1). Flammulated Owls were detected on 44 of the 68 routes (65%). On routes where owls were detected, mean owl densities (# singing males/40 ha) for the 3 study sites ranged from 0.28 to 0.52 (Table 1). The earliest and latest dates that owls were detected were 10 May 1990 and 23 July 1990, respectively. Other owl species detected on these surveys included Great Horned Owl (*Bubo virginianus*), Long-eared Owl (*Asio otus*), Northern Saw-whet Owl (*Aegolius acadicus*), and Barred Owl (*Strix varia*) on the SNF; Short-eared Owl (*Asio flammeus*), Northern Pygmy Owl (*Glaucidium gnoma*), Great Gray Owl (*Strix nebulosa*), Barred, Great Horned, Long-eared, and Northern Saw-whet Owls on the PNF-HCNRA; and Great Horned, Northern Saw-whet, and Barred Owls on the NPNF.

We compiled 74 additional distributional records of Flammulated Owls in Idaho (Appendix A, Fig. 1). Eighteen of these records came from additional surveys conducted by Payette National Forest staff in Adams County within the PNF-HCNRA study site. For the 55 records that contained habitat information, 43 (78%) were from areas dominated by ponderosa pine, Douglas-fir, or a combination of both species. These records were distributed throughout the montane forest portions of the state. The earliest record was dated 30 March and the latest 17 October.

Habitat Characteristics

STAND LEVEL.—We measured stand-level habitat characteristics at 12 owl locations on the PNF-HCNRA and 5 locations on the NPNF study sites (Table 2). Forty percent of

TABLE 1. Flammulated Owl survey results on the Salmon (SNF), Payette–Hells Canyon NRA (PNF-HCNRA), and Nez Perce (NPNF) national forests, Idaho, 1990–1992.

Survey site	Survey dates	Number survey routes	Number routes with owls	Owl density[a] (owls / 40 ha) $\bar{x}$	s	Range
SNF	9 May–23 July 1990	20	16	0.28	0.29	0.04–1.25
PNF-HCNRA	22 May–11 July 1991	38	22	0.31	0.22	0.09–0.84
NPNF	11 May–10 July 1992	10	6	0.52	0.29	0.25–0.98
Total		68	44			

[a] Density calculated only for survey routes on which owls were detected.

owl locations were located on upper slopes, 25% on ridges, 25% on mid-slopes, and 10% on valley bottoms. Elevations for the 17 locations averaged 1561 m ($s_{\bar{x}} = 39.8$) on the PNF-HCNRA study site and 1504 m ($s_{\bar{x}} = 27$) on the NPNF site.

Either ponderosa pine or ponderosa pine mixed with Douglas-fir dominated the vegetation at owl locations on the NPNF and PNF-HCNRA sites (Table 2). Cover estimates for canopy, shrub, and ground vegetation layers were similar in the 2 study sites. Tree density was approximately 500/ha on both areas, and mean dbh values for all trees was 32 cm for the PNF-HCNRA and 31 cm for the NPNF.

Although we did not collect habitat data on the SNF study site, Forest Service timber crews had previously inventoried 26 of the 67 stands that contained owl locations in our surveys on the SNF (Atkinson and Atkinson 1990). All but one of these stands were dominated by Douglas-fir, ponderosa pine, or a mix of both. The exception was a stand of subalpine fir *(Abies lasiocarpa)* / beargrass (*Xerophyllum tenax*). Average dbh values were 28.3 cm ($s = 8.1$) for Douglas-fir and 38.1 cm ($s = 15.0$) for ponderosa pine.

MACROHABITAT.—We measured macrohabitat features of Flammulated Owls at 9 owl locations on the PNF-HCNRA study site. Within the nine 50.3-ha macrohabitat plots on the PNF-HCNRA, mean percent cover of forest >120 yr old was 31% ($\bar{x} = 16$ ha, $s = 18$). Mean cover of timber stands 50–100 yr old was 30% ($\bar{x} = 15$ ha, $s = 10$), followed by natural openings at 12% ($\bar{x} = 6$ ha, $s = 9$) and selective cuts at 12% ($\bar{x} = 6$ ha, $s = 5$). Clearcuts, immature forest, open woodlands, and other unclassified areas were relatively low in cover (<2 ha each).

DISCUSSION

Our surveys and compilation of distributional records of Flammulated Owls show that this species inhabits montane forests throughout Idaho (Fig. 1). In our surveys Flammulated Owls were not detected in only 1 area—the South Fork Clearwater River of NPNF. A lack of snags and large-diameter ponderosa pine trees due to timber harvest and firewood cutting may have made this area less suitable to Flammulated Owls.

Densities of responding owls in Idaho were within the range of 0.03–1.09 owls/40 ha reported in northern California (Marcot and Hill 1980) during similar aural surveys. Although we recorded high densities on some survey routes, average regional densities were less than estimates of 0.7 males/40 ha recorded by Howie and Ritcey (1987) in British Columbia. However, caution should be exercised in comparing these results because the actual areas surveyed vary due to differences in wind, topography, individual and seasonal variation in owl responses, and observer bias. Furthermore, estimates of density calculated with a theoretical radius of coverage around broadcast stations may be biased upward because of owls moving into "survey areas" in response to broadcasted calls and owls following surveyors from 1 broadcast station to another (R. Reynolds personal communication).

Most detections of Flammulated Owls in Idaho were in mature to older stands of ponderosa pine mixed with Douglas-fir. However, several records of Flammulated Owls that we compiled from areas outside our study sites represented owls heard calling (and nesting in 1 case) from pure stands of Douglas-fir or aspen, particularly in southeastern Idaho where

TABLE 2. Habitat characteristics at Flammulated Owl locations on the Payette National Forest–Hells Canyon National Recreation Area (PNF-HCNRA; n = 12) and the Nez Perce National Forest (NPNF; n = 5), Idaho, 1991–1992.

Location	Tree density [#/ha (s)]	$\bar{x}$ dbh [cm (s)]	Percent cover [$\bar{x}$ (s)] Canopy	Shrub	Ground	Dominant vegetation type (% of plots) PIPO[a]/PSME	PIPO	Other
PNF-HCNRA	498 (294)	32 (5)	64 (12)	16 (13)	49 (10)	25	50	25[b]
NPNF	494 (1426)	31 (27)	52 (30)	21 (20)	39 (18)	84	—	16[c]

[a] PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii*.

[b] This category represents plots dominated by *Populus tremuloides* or *Abies grandis*.

[c] This category represents plots dominated by *P. menziesii* or *Larix occidentalis*.

ponderosa pine is absent. In addition, we recorded several instances of owls calling from stands of grand fir (*Abies grandis*). These patterns are consistent with other studies which indicate that while open ponderosa pine forests represent the most common nesting habitat, other forest types are used. Aspen is a frequent component of nesting habitat in Colorado and Nevada (Reynolds and Linkhart 1987b, McCallum 1994b), and owls have nested successfully in selectively harvested Douglas-fir stands in British Columbia (Howie and Ritcey 1987).

Our habitat analyses indicated Flammulated Owls in western and north central Idaho use forest stands with mature to old ponderosa pine and Douglas-fir, multiple canopy layers, low tree densities, moderate to low canopy closure, and moderate ground cover. These habitat features are characteristic of old ponderosa pine forests and are similar to those reported for this species elsewhere in its breeding range (Goggans 1986, McCallum and Gehlbach 1988, Bull et al. 1990, Reynolds and Linkhart 1992). However, because habitat measurements were taken only at occupied sites and survey routes were chosen to maximize the amount of old or mature ponderosa pine, habitat selection cannot be inferred from these data.

Marshall (1939) suggested that the Flammulated Owl may be the most common raptor in pine forests of the western United States. Our surveys in Idaho indicate Flammulated Owls are abundant in particular habitats, but no comparative data exist for densities of other forest raptors. Whether the populations we studied are increasing, stable, or declining is not known, nor is it known for the species throughout its range (McCallum 1994c).

There is, however, some concern for the species' future. Ponderosa pine forests in Idaho and elsewhere are declining due, in part, to fire suppression and timber harvest. Little is known about the effects of these management activities on Flammulated Owls at either the stand level through changes in forest structure or at the landscape level through habitat fragmentation (McCallum 1994b, 1994c). Biologists and land managers would greatly benefit from more research aimed at a greater understanding of the habitat requirements of this forest owl and the impacts that various silvicultural treatments might have on these requirements.

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(Appendix A begins on the following page.)

APPENDIX A

Summary of all Flammulated Owl records and observations in Idaho not recorded during surveys conducted at 3 study sites (SNF, PNF-HCNRA, NPNF) and reported in this paper. More detail on these records is provided by the Idaho Conservation Data Center (IDCDC), Idaho Department of Fish and Game, Box 25, Boise ID 83707.

Date	Observer	Habitat[a]	County	Source of data
22 September 1890	Merriam		Blaine	Burleigh 1972
28 September 1914	Rust		Kootenai	Burleigh 1972
Summer 1973	Trost	urban	Bannock	ISU Museum[b]
22 September 1977	Powers	urban	Ada	AB 32:234[c]
23 September 1977	Jeppson	urban	Bannock	AB 32:234
September 1978	Jeppson	urban	Bannock	AB 33:197
7 May 1980	Humble		Shoshone	IDCDC
5 October 1980	Trost	DF	Bannock	ISU Museum
1981–1985	Hayward	PP	Idaho	Hayward and Garton 1988
June 1982	Hayward	DF/PP	Boise	Hayward 1986
26 August 1982	Jeppson	urban	Bannock	AB 37:204
26 September 1986	Jeppson	urban	Bannock	ISU Museum
6 July 1987	Uhnschneider	DF	Elmore	IDCDC
3 October 1987	Dudley		Gem	Stephens and Sturts 1991[d]
5 July 1988	Hansen		Kootenai	AB 42:1319
September 1988	Trost	urban	Bannock	ISU Museum
17 October 1988	Hansen		Kootenai	AB 43:138
July 1989	Trost	DF	Bannock	IDCDC
May 1990	Trotter		Twin Falls	AB 44:467
22 May 1990	Trost	DF	Bannock	AB 44:467
14 June 1991	Atkinson	DF	Fremont	IDCDC
19 June 1991	Patla	aspen	Teton	IDCDC
May 1991	Trotter		Twin Falls	AB 45:475
31 May 1991	Trochlell	DF	Camas	IDCDC
1 June 1991	Trochlell		Twin Falls	IDCDC
July 1991	Trost	DF	Bannock	AB 45:1140
18 September 1991		urban	Bingham	ISU Museum
12 April 1992	Leppert	PP	Adams	IDCDC
21 April 1992	McCammon	PP	Boundary	IDCDC
24 May 1992	Gray	DF/PP	Idaho	IDCDC
29 May 1992	Baerlocker		Idaho	Stephens and Sturts 1991
30 May 1992	Uhnschneider		Boise	IDCDC
June 1992	Leppert	DF/PP	Adams	IDCDC
16 June 1992	Leppert		Adams	IDCDC
18 June 1992	McCammon	PP	Boundary	IDCDC
18 June 1992	Walker	DF/PP	Adams	IDCDC
18 June 1992	Leppert	DF/PP	Adams	IDCDC
19 June 1992	Leppert	DF/PP	Adams	IDCDC
20 June 1992	Leppert	DF/PP	Adams	IDCDC
21 June 1992	Leppert	DF/PP	Adams	IDCDC
22 June 1992	Riley	PP	Bonner	IDCDC
23 June 1992	Atkinson	aspen	Bonneville	IDCDC
24 June 1992	Richards	PP	Adams	IDCDC
7 July 1992	Leppert	DF/PP	Washington	IDCDC
14 July 1992	Skinner	DF/PP	Washington	IDCDC
17 July 1992	Belt	grand fir	Idaho	IDCDC
17 July 1992	Leppert		Idaho	IDCDC
27 July 1992	Naderman		Bonneville	IDCDC
17 August 1992	Feldham	DF	Bear Lake	Stephens and Sturts 1991
5 October 1992	Svingen		Benewah	AB 47:122
30 March 1993	Leppert	DF/PP	Adams	IDCDC
23 April 1993	Wessman	DF/PP	Boise	IDCDC
5 May 1993	Trost	DF	Bannock	AB 46:453
26 May 1993	Evans		Adams	IDCDC
16 June 1993	O'Neill	PP	Adams	IDCDC
17 June 1993	Johnston	DF	Idaho	IDCDC
23 June 1993	Holliday	DF/PP	Adams	IDCDC
24 June 1993	Holliday	DF/PP	Adams	IDCDC
24 June 1993	Holliday	DF/PP	Adams	IDCDC

APPENDIX A

Continued.

Date	Observer	Habitat[a]	County	Source of data
14 July 1993	Johnston	PP	Idaho	IDCDC
14 July 1993	Cassirer		Nez Perce	IDCDC
15 July 1993	Robinson	aspen	Bear Lake	IDCDC
3 May 1994	Garwood	DF	Camas	IDCDC
24 May 1994	Dhaenens	PP	Idaho	IDCDC
26 May 1994	Garwood	DF/aspen	Blaine	IDCDC
June 1994	Stotts	DF/PP	Idaho	Clearwater NF
26 June 1994	Holliday	PP	Adams	IDCDC
28 June 1994	Leppert	DF/PP	Adams	IDCDC
28 June 1994	Holliday	PP	Adams	IDCDC
28 June 1994	Belt	grand fir	Idaho	IDCDC
October 1994			Jefferson	ISU Museum
17 May 1995	Wondolleck	DF/PP	Shoshone	IDCDC
8 June 1995	Faike		Blaine	IDCDC
27 June 1995	McCammon	PP	Valley	IDCDC

[a] Douglas-fir = DF, ponderosa pine = PP, Douglas-fir and ponderosa pine = DF/PP.

[b] ISU = Idaho Museum of Natural History, Idaho State University, Pocatello.

[c] AB= American Birds.

[d] Stephens and Sturts 1991 = a latilong database developed by D. A. Stephens and maintained by the Idaho Department of Fish and Game.

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DEN AND RELOCATION SITE CHARACTERISTICS AND HOME RANGES OF *PEROMYSCUS TRUEI* IN THE WHITE MOUNTAINS OF CALIFORNIA

Linnea S. Hall[1] and Michael L. Morrison[2]

ABSTRACT.—We used radio telemetry to describe nighttime movements and daytime den sites of pinyon mice (*Peromyscus truei*) in the White Mountains of California, 1991–1993. Characteristics of nighttime relocations and den sites for mice concurred with previously reported habitat-use information for the species and supported the claim that pinyon mice use multiple daytime sites. However, males and females were associated with different habitat characteristics at den sites, indicating differential microhabitat selection by the sexes, perhaps related to reproductive constraints on females. Pinyon mice also exhibited high variability in den site habitat use in the summer, but low variability in the fall and winter. The dens of male mice were farther apart than those of females, and home range areas averaged 2.9 ha (s = 4.27 ha) for 8 males, and 0.8 ha (s = 0.76 ha) for 7 females (overall $\bar{x}$ = 1.7 + 2.97 ha). These areas were larger than those reported for other species of *Peromyscus*. The combined effects of drought and reduced food availability may have contributed to the larger areas used.

Key words: den sites, habitat use, Peromyscus truei, *pinyon mouse, radio telemetry, White Mountains.*

Several studies have described home range sizes of *Peromyscus* species, especially as they are affected by food availability, population densities, interspecific competition, and habitat use (Taitt 1981, Wolff 1985, Douglass 1989). Researchers commonly used live-trapping data to determine home ranges and core areas (e.g., Douglas 1969, Meserve 1977, Merritt and Merritt 1978, O'Farrell 1978, Ribble and Samson 1987) but recently have increased their use of radio telemetry for this purpose (Madison 1977, Mineau and Madison 1977, Douglass 1989). Many studies of home ranges and habitat use have been conducted on *P. maniculatus* and *P. leucopus* (Wolff 1989:285), but only a few of these have detailed den or nest site characteristics or telemetry relocation characteristics (Madison 1977, Klein and Layne 1978, Stah 1980, Wolff and Hurlbutt 1982, Wolff and Durr 1986, Douglass 1989, Frank and Layne 1992). Most information on mouse dens comes from older studies in which researchers located and excavated sites they came upon by chance (e.g., McCabe and Blanchard 1950:21, Douglas 1969). Telemetry allows the location of dens without disturbance and the determination of the frequency with which mice return to den sites. In addition, telemetry may permit more accurate descriptions of habitat use than would live- or snap-trapping stations because the latter can bait animals into them and thus not necessarily represent the habitat that is typically used (Cranford 1977, Douglass 1989).

Because of these advantages, we used telemetry to describe den sites and home range sizes of pinyon mice (*P. truei*) in the White Mountains of California. Pinyon mice are common in the western U.S. (Hoffmeister 1981), but they have not figured prominently in habitat-use studies relative to other *Peromyscus* species (but see Douglas 1969, Scheibe 1984a, Ribble and Samson 1987, Scheibe and O'Farrell 1995). Therefore, we initiated this study to discern habitat use by *P. truei* in the White Mountains.

STUDY AREA

The White Mountains are located east of Bishop, Inyo County, California, and rise from 1515 to 4245 m elevation (T7S, R35E, sec. 30–32). The dominant vegetation between 2090 and 2725 m elevation is pinyon-juniper (*Pinus monophylla–Juniperus osteosperma*) woodland. This woodland is xeric with sparse vegetative cover and warm, dry summers. Snow cover and rainfall usually last from November through May, with afternoon thunderstorms in late summer (unpublished data). The only tree species in the woodland are pinyon and juniper; dominant shrubs are big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia glandulosa* and *P. tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*C. viscidiflorus*), Mormon tea (*Ephedra viridis*), cactus (*Opuntia* and *Echinocereus* spp.), and squaw apple (*Peraphyllum* sp.; Dedecker 1984). More detailed descriptions of the study area are provided in Hall (1992).

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METHODS

Radio Telemetry

To catch mice for attachment of radio transmitters, we set Sherman live-traps (7.6 × 8.9 × 22.9 cm) on two 4-ha grids and four 1.8-ha grids at about 2500 m elevation in the pinyon-juniper vegetation. The large grids (pinyon and cedar; 81 traps/grid with 25-m spacing) were established in 1988 as part of a long-term project on mice; the small grids (100 traps/grid with 15-m spacing) were established in 1991 as control grids used in an experimental study (Morrison 1988, Hall 1992). These grids were used for a total of 870 trap-nights from 1991 to 1993 specifically to provide animals for telemetry. Additional trapping was conducted on the sites to determine population abundances and habitat use (Morrison et al. 1991, Hall 1992).

We checked traps between midnight and first light, rather than at dawn, to minimize the stress of affixing transmitters on nocturnal mice. To identify species with surety, we examined specimens at the Museum of Vertebrate Zoology, University of California, Berkeley, and compared them with specimens we collected from 1988 to 1991 (Morton et al. 1995). In addition, there were only 2 species of *Peromyscus* inhabiting our study area (*P. truei* and *P. maniculatus*), which were not difficult to distinguish from each other. Thus, we are confident in our identifications of pinyon mice.

We radio-tagged subadult and adult mice for which transmitters were ≤ 10% of their body masses (transmitters, with acrylic potting, averaged 2.0 g; SM-1 Mouse Style, AVM Instrument Co., Livermore, CA). Ages of animals were distinguished based on our previous work with the populations (Morrison et al. 1991, Morrison and Hall unpublished data): subadults were born the current year and were nearly fully molted, weighing 14.1–18.0 g; adults were born the previous year and were fully molted, weighing ≥ 18.1 g.

We anaesthetized each mouse with Metofane and removed a 2.0 × 1.0-cm patch of dorsal fur from between the shoulders, down to just above the skin. We then adhered the transmitter to the back with cyanoacrylate. Each mouse was kept in a protected box for 10–15 min and released at its initial point of capture after its recovery from anaesthesia.

We obtained the 1st relocation (fix) on each radio-tagged animal during the daytime about 6 h after the radio was attached. We used a portable receiver (Telonics, Inc., Mesa, AZ, and Communications Specialists, Inc., Orange, CA) and 2- and 3-element Yagi antennas. After locating a signal, we walked to the fix or den site and recorded the azimuth and distance (m) to a trap location on the grid, and then determined coordinates for the fix location. We obtained 1–3 fixes every night, and 1 den site was recorded every day for each individual as long as the transmitter remained attached. Forty-three percent of the telemetry relocations were collected when there was no or very little moonlight (i.e., around the time of a new moon), and only 16% were collected when the moon was 60–100% full and overhead. At night we homed in (White and Garrott 1990:42) on each mouse by following the transmitted signal until we were within 10 m of the animal. This was accomplished by keeping our lights off or at low power and minimizing all noise as we approached radio-tagged individuals.

We radio-tagged a total of 30 pinyon mice from July 1991 through July 1993: of these, 21 were tagged between July and December 1991, 2 in January 1992, and 7 between May and July 1993. Sixteen of the mice were males and 14 females; 20 were adults and 10 subadults. Characteristics of nighttime relocations and daytime den relocations were described for 26 and 25 animals, respectively. To assess habitat characteristics we recorded 11 substrate types in, on, or under which each fix occurred (Table 1). We also recorded the plant species nearest the fix site (i.e., the primary plant); the plant species near the primary plant, but farther from the fix site (i.e., the secondary plant); and the size (small [≤ 2 m], medium [2.1–4.9 m], or large [≥ 5 m]) of the nearest plant.

TABLE 1. Substrates used for den sites by pinyon mice, and/or associated with relocation sites of mice in the White Mountains of California, 1991–1993.

Substrate
Dead tree base and/or exposed roots
Live tree base
Live tree (up in)
Rock (outcrop, slab, shelf)
Downed log
Snag
Tree trunk
Dead branch (or mistletoe ball) in live tree
Shrub base
Hole
Stump

Analyses

DEN AND RELOCATION SITES.—We used loglinear analyses (Sokal and Rohlf 1981:747) to test for patterns of association among combinations of plant and substrate variables recorded at nighttime and daytime relocation sites. For these analyses we evaluated each combination of dependent and independent categorical variables (e.g., sex of mouse by substrate, age of mouse by nearest plant, season by plant size). A loglinear analysis tests for independence of categories by calculating odds ratios from residuals of observed and expected values, and then determining the goodness of fit of the resulting ratio model (Sokal and Rohlf 1981:748). The analysis is useful for uncovering relationships among variables in a multiway crosstabulation, similar to multiple comparison procedures for multiway analyses of variance.

HOME RANGES.—We used program McPAAL (vers. 1.22, M. Stuwe and C. E. Blohowiak, Conservation and Research Center, National Zoological Park, Smithsonian Institution, Washington, DC) to determine the home range sizes of mice for which we collected ≥ 8 total fixes. Although our relocation data were few per mouse, we used harmonic mean (HM) analyses (Dixon and Chapman 1980) to calculate home range sizes for each mouse individually. This method includes less unused space in the home range area than the minimum convex polygon method (Hayne 1949), and it has greater utility because it approximates the size of the activity centers of animals (i.e., areas with highest activity intensities).

HM values of the mice did not differ significantly among the 6 grids (1-way analysis of variance [ANOVA, Zar 1984:163] $F = 0.71$, $P = 0.57$, df = 3, 4), and so we pooled all grids together to make sample sizes larger for the other analyses. We then conducted *t* tests (Zar 1984:126) of home range sizes between sexes, and ANOVAs of home ranges among seasons (summer, July–August; fall, September–October; winter, December–January).

For all statistical analyses we used SPSS/PC+ (Norusis 1992) and considered $P \leq 0.05$ to be significant.

RESULTS

Nighttime Relocation Characteristics

Most nighttime relocation sites were associated with singleleaf pinyon trees (42%), Utah juniper trees (31%), bitterbrush (11%), and rock outcrops (8%). Across all grids, male mice used shrub bases and downed logs less than expected, whereas female mice used these substrates more than expected (loglinear analysis, $G = 18.2$, $P = 0.002$, df = 8). Adult mice used shrub bases less than expected, subadult mice more than expected ($G = 19.6$, $P = 0.01$, df = 8). Subadult mice were associated with juniper trees more often than expected, whereas adult mice again showed the opposite pattern ($G = 19.1$, $P = 0.004$, df = 6).

Den Site Characteristics

The average distance moved between consecutive den sites was 47.0 m ($s_{\bar{x}} = 10.60$ m, $n = 17$ mice with ≥ 2 den sites). Males moved an average of 82.0 m ($s_{\bar{x}} = 16.65$ m, $n = 6$), and females moved 31.0 m ($s_{\bar{x}} = 13.76$ m, $n = 8$); the difference between the sexes was significant ($t = 2.38$, $P = 0.04$, df = 12). Males moved a maximum of 160 m and females a maximum of 126 m between consecutive dens. The minimum movement was 0 m (i.e., when mice stayed in the same den ≥ 2 nights in a row).

We recorded data for 72 den sites (60 in 1991, 2 in 1992, and 10 in 1993). Animals with ≥ 2 den sites averaged 3.0 ± 1.8 different den locations during the time we followed them. Most dens were located in or under rock ledges, outcrops, slabs, or shelves (28%), and in live trees (25%). They were secondarily found in downed logs, dead branches of otherwise live trees, and at shrub bases (8% each). The nearest plants to these dens were most commonly pinyon pines (50%) and junipers (32%).

Male mice used live tree bases more than expected and dead branches in live trees less

TABLE 2. Vegetative characteristics associated significantly more or less often than expected with den sites used by pinyon mice in the White Mountains, California, 1991–1993.

Sex	Variable	Use[a]
MALE		
	Live trees	>
	Dead branches in live trees	<
	Pinyon trees	>
	Bitterbrush shrubs	<
	Small trees	<
	Large trees	>
FEMALE		
	Live trees	<
	Dead branches in live trees	>
	Pinyon trees	<
	Bitterbrush shrubs	>
	Small trees	>
	Large trees	<

[a] Use: > = use of variable by mice was significantly greater than expected; < = use was significantly less than expected (loglinear analysis, $P \leq 0.05$).

TABLE 3. Vegetative characteristics associated more or less often than expected with den sites used by pinyon mice in summer, winter, and fall 1991–1993.

Variable	Summer use[a]	Fall use	Winter use
Live trees	>	<	ns[b]
Shrub bases	>	<	ns
Holes	>	<	ns
Snags	<	ns	>
Pinyon trees	>	<	ns
Bitterbrush shrubs	<	>	ns
Small trees	<	>	ns
Medium trees	>	<	ns

[a] Use: > = use of variable by mice was significantly greater than expected; < = use was significantly less than expected (loglinear analysis, $P \leq 0.05$).

[b] ns = nonsignificant result in loglinear analysis ($P > 0.05$).

than expected, whereas females showed the opposite pattern (loglinear analysis, $G = 25.7$, $P = 0.004$, df = 10; Table 2). Male dens were associated more commonly with pinyon trees and less commonly with bitterbrush shrubs than expected, whereas females again showed the opposite pattern ($G = 10.6$, $P = 0.03$, df = 4). Finally, female dens were associated with small trees more often and large trees less often than expected; males showed the opposite pattern of habitat use ($G = 11.8$, $P = 0.003$, df = 2; Table 2).

There were also differences among age classes: adult mice used dead branches in live trees less than expected, but subadult mice used them more than expected ($G = 23.5$, $P = 0.009$, df = 10). Adult mice also used medium-sized trees less often, whereas subadult mice used them more often ($G = 7.1$, $P = 0.03$, df = 2).

Among seasons (summer, fall, winter), live tree and shrub bases and holes were used more often, and snags were used less often, during summer. In fall, live tree and shrub bases and holes were used in the opposite pattern; in winter, snags were used in the opposite pattern ($G = 34.4$, df = 20, $P = 0.02$; Table 3). Also in summer, den sites were associated with pinyons more than expected and with bitterbrush less than expected; in fall, the opposite pattern was exhibited ($G = 17.7$, df = 6, $P = 0.007$). Finally, small trees were used less than expected and medium-sized trees more than expected in summer; the opposite pattern occurred in fall ($G = 17.4$, df = 4, $P = 0.002$; Table 3).

Home Ranges

We analyzed a total of 134 fixes among 30 radio-tagged mice, ranging from 4 to 31 fixes per animal ($\bar{x} = 10 \pm 5.8$ per animal). Fixes were collected about 10 h apart ($s = 2.1$ h), over an average of 5 d ($s = 3.1$ d).

For animals with ≥ 8 total fixes ($n = 15$; 7 females, 8 males), home range sizes did not differ among seasons for males ($F = 1.82$, $P = 0.26$, df = 2, 5) or females ($F = 4.77$, $P = 0.09$, df = 2, 4). Harmonic mean areas averaged 1.7 ha ($s = 2.97$ ha) for all mice combined. Home range sizes of male mice did not differ from those of female mice in any season (t tests, P values ≥ 0.08). Combined across all seasons, male HM areas averaged 2.9 ± 4.27 ha and female HM areas averaged 0.8 ± 0.76 ha. Seasonal home range sizes ranged from 0.1 ha (fall males and winter females) to 5.5 ha (summer males; Table 4).

DISCUSSION

Characteristics of the habitat used by pinyon mice at night and during daytime denning concur with previously published data regarding habitat use for this species (Hoffmeister 1951:34, 1981, Douglas 1969:461, Ribble and Samson 1987). We also substantiated the claim that pinyon mice use multiple daytime sites (Douglas 1969:464), a characteristic shared by several other species of *Peromyscus* (Stickel 1968:388). However, male and female pinyon mice exhibited differential habitat use at daytime sites: males used tall pinyon trees and the bases of

TABLE 4. Seasonal differences in home range sizes of male and female pinyon mice in the White Mountains, California, from 1991 to 1993.

		Harmonic mean values		
Sex	Season	$\bar{x}$ (ha)	*s*	*n*
MALE				
	Summer	5.5	4.95	4
	Fall	0.1	0.04	2
	Winter	0.5	0.59	2
	Overall	2.9	4.27	8
FEMALE				
	Summer	1.6	0.67	2
	Fall	0.7	0.53	3
	Winter	0.1	0.06	2
	Overall	0.8	0.76	7

live trees, whereas females used dead branches (and mistletoe balls) in small but otherwise live trees, and also bitterbrush shrubs. Scheibe and O'Farrell (1995) likewise found differences in habitat use between male and female pinyon mice in California and suggested that this was related to the constraints of reproduction on females versus the relative lack of constraints on males. On the other hand, Scheibe (1984b) found no significant differences in the home range habitat characteristics of male and female pinyon mice in California. However, because he considered only the species of plants present, it was not surprising that both sexes were associated with the same vegetation.

We also observed seasonal variation in densite use, with greater variability in substrate use in the summer than in the fall and winter. Scheibe and O'Farrell (1995) similarly found that female pinyon mice were consistently associated with particular habitat characteristics during reproductive months. Males, however, were associated with a wide breadth of habitat characteristics, especially in the spring and summer, but did show increased habitat specificity in the fall and winter. Additionally, the den sites of male pinyon mice were located farther apart than the dens of females. Males and females also tended toward having different home range sizes, similar to the findings of Scheibe (1984b). As with habitat use, these sexual differences may result from the relative selectivity of male and female mice based on their needs for finding mates and for tending nests, respectively (Scheibe and O'Farrell 1995). Increased habitat specificity in the fall and winter, as we observed, could be tied to males' reduced need to move widely in search of mates, changes in food availability for both sexes, and/or changes in environmental temperatures, among other factors (e.g., Scheibe 1984a).

Our average home range area estimate for all *P. truei* combined was 1.7 ha, which was much larger than telemetry estimates for *P. leucopus* by Madison (1977; 0.1 ha), Mineau and Madison (1977; 1.1 ha), and Wolff (1985; 0.06 ha), and for *P. maniculatus* by Wolff (1985; 0.05 ha). Previous estimates for pinyon mice based on live-trapping were also smaller, ranging from 0.43 (Douglas 1969:439) to 0.48 ha (Scheibe 1984b) for adult male pinyon mice (vs. our 2.9 ha), and from 0.28 (Scheibe 1984b) to 0.37 ha (Douglas 1969) for adult females (vs. our 0.8 ha).

We think the large home range estimates for pinyon mice in the White Mountains in this study could have been due to 3 interacting factors. First, drought may have influenced how pinyon mice utilized space. A recent California drought lasted from 1986 to the winter of 1992–93, and pinyon mice were at low abundances and experiencing low and abbreviated productivity during this period (Morrison et al. 1991, Morton et al. 1995, Morrison and Hall submitted manuscript). Second, the drought was combined with poor pinyon seed crops in the White Mountains, which probably further contributed to reducing the densities of mice (Morrison et al. 1991, Morrison and Hall submitted manuscript). With decreased food and water availability, pinyon mice may have had to forage widely, leading to the large home ranges we observed.

Finally, although some authors have suggested that a large number of live-trapping recaptures in a trap session adequately represent microhabitat and space use by small mammals (Wolff 1985, Desy et al. 1989), others have suggested that radio telemetry provides a more complete and accurate assessment of these parameters (Cranford 1977, Bergstrom 1988, Douglass 1989). In our study, mice used an average of 1.7 ha over about 5 d, and many mice used areas off the 1.8- and 4-ha grids (Hall 1992, Hall and Morrison submitted manuscript). This suggests that if we had relied only on trapping data to estimate the home range sizes of mice, we would have underestimated the areas used. The large home ranges were probably not an artifact of the radio transmitters;

studies on birds have demonstrated that transmitters tend to cause reduced home range sizes rather than larger home range sizes (e.g., Hooge 1991), if there are any effects at all. The choice of whether or not to use telemetry therefore has important implications for the determination of habitat use and may also influence calculations of survival, immigration, trappability (e.g., Krebs and Boonstra 1984), and dispersal of small mammals in grid-based studies.

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LATE FALL AND EARLY SPRING BIRD OBSERVATIONS FOR MULEGÉ, BAJA CALIFORNIA SUR, MEXICO

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ABSTRACT.—Observational data from spring and fall 1996 and spring 1997 for the region near Mulegé, Baja California Sur, Mexico, are summarized in tabular form. In addition, new or noteworthy data for 17 species are annotated to provide clarification of previously published records. A uniquely plumaged bird, too far south for a female American Robin (*Turdus migratorius*) in basic plumage and too far north for the endemic "San Lucas" Robin (*Turdus migratorius confinis*) and intermediate in coloration between the two, was recorded. Range expansions are documented for several species including European Starling (*Sturnus vulgaris*), Anna's Hummingbird (*Calypte anna*), Western Meadowlark (*Sturnella neglecta*), White-faced Ibis (*Plegadis chichi*), and White-fronted Goose (*Anser albifrons*). Least Grebes (*Tachybaptus dominicus*), a species of concern which is apparently declining in numbers, and Belding's Yellowthroat (*Geothlypis beldingi*), a species endemic to Baja California Sur, were observed in the freshwater marsh during all 3 study periods.

Key words: Baja California Sur, Mexico; Mulegé, bird records, range expansion, desert oasis.

The avifauna of Baja California (hereafter BC), the second longest and most geographically isolated peninsula in the world (Grismer and McGuire 1993), is one of the most interesting, yet poorly studied, in North America (Wilbur 1987, Howell and Webb 1995). Late 19th and early 20th century natural history work in BC has been summarized by E. D. Nelson (1921) and J. Grinnell (1928). Much of the recent ornithological effort has been concentrated in either the coast and mountains of northern BC (Kiff et al. manuscript in preparation, Patten et al. 1993, Unitt et al. 1995), lagoons of the Pacific coast (Massey and Palacios 1994), offshore islands (Anderson 1983, Cody 1983), or southernmost regions from La Paz to the cape (Rodriquez-Estrella and Rivera-Rodriquez 1992, Carmona et al. 1994, Guzman et al. 1994). This report summarizes early spring 1996 and 1997 and late fall 1996 observations for the area near Mulegé, Baja California Sur (hereafter BCS).

Mulegé is located on the east coast of BCS north of Bahía Concepción and south of Santa Rosalía, straddling 26°53′N, 111°58′W (Fig. 1). Vehicular access is by means of Mexico Highway 1, a reasonably maintained 2-lane asphalt road passable during all but the wettest seasons, approximately 800 km south of Tijuana, Baja California Norte (hereafter BCN), and 500 km north of the cape. A landing strip at the Hotel Serinidad, approximately 2 km east of the town, supports small aircraft, while the nearest commercial air service is to Loreto, approximately 132 km south. Its distance from both the northern and southern population centers makes Mulegé accessible only to hardy travelers.

The area features both a brackish water tidal estuary, Rio Mulegé, and a small, year-round spring-fed freshwater lagoon. The former is small, <3 km long, runs primarily west to east, and includes a poorly developed saltwater marsh of cordgrass (*Spartina foliosa*, Gramineae), glasswort (*Salicornia bigelovii*, Chenopodiaceae), and saltwort (*Batis maritima*; plant names follow Roberts [1989]). A narrow mangrove community, principally black mangrove (*Avicennia germinans*, Avicenniaceae) and red mangrove (*Rhizophora mangle*, Rhizophoraceae), occurs irregularly along the estuary and on several small islands within its boundaries. Above the high tide zone are scattered stands of mangle dulce (*Maytenus phyllanthoides*, Celastraceae). Lining the southern edge of the estuary are several "retirement" communities consisting of permanent houses and semipermanent domiciles formed by modifying various types of motor homes and trailers. Many residents provide supplemental food for birds in the form of typical "backyard" grain feeders and hummingbird feeders filled with sugar water. Associated with these communities are numerous

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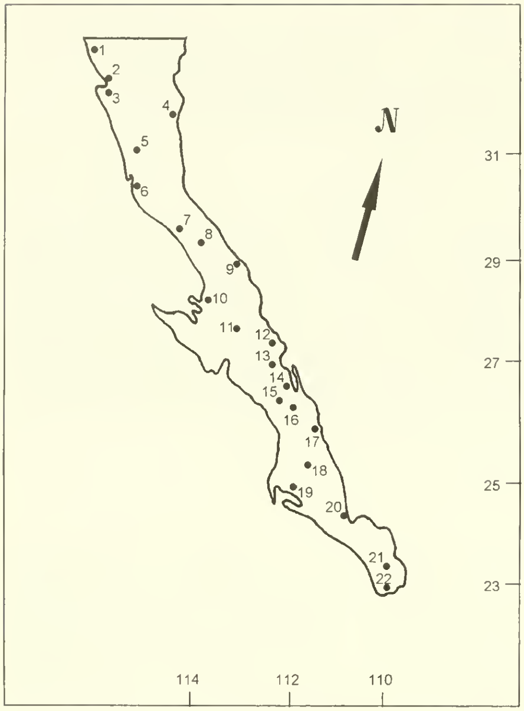

Fig. 1. Outline map of 2 states in Los Estados Unidos de Mexico, Baja California Norte and Baja California Sur, showing approximate position of prominent locations: 1, Tijuana; 2, Ensenada; 3, Maneadero; 4, San Felipe; 5, Santo Domingo; 6, Bahía de San Quintín; 7, El Rosario; 8, Cataviña; 9, Bahía de Los Angeles; 10, Guerrero Negro; 11, San Ignacio; 12, Santa Rosalía; 13, Mulegé; 14, Bahía Concepción; 15, La Purísima; 16, Comondú; 17, Loreto; 18, Ciudad Insurgentes; 19, Bahia Magdalena; 20, La Paz; 21, La Laguna; 22, San José del Cabo.

ornamental plantings and scattered palms including native Mexican fan palm (*Washingtonia robusta*, Arecaceae) and introduced date palm (*Phoenix dactylifera*, Arecaceae). Dense stands of these species are locally referred to as the "palmar."

The freshwater lagoon, approximately 1.5 km long and 10–30 m wide depending on season, is formed by damming the main spring, primarily to prevent tidal saltwater contamination. It supports a small community, a plantation of date palms, a dense stand of rush (*Juncus* sp., Juncacae), and limited citrus and mango orchards. The lagoon is highly impacted by domestic cattle and pigs, which run freely and have trampled significant portions of the edge habitat. Away from the water, habitat abruptly transforms into sarcocaulescent desert (Wiggins 1980) dominated by *Cercidium*, *Bursera*, *Pachycereus*, and *Opuntia* (Wilbur 1987). To the west of the lagoon an arroyo meanders through the center of a broad valley. The arroyo contains water only during seasonally heavy rains. Portions of the valley are heavily irrigated with ancestral water and support citrus orchards, corn, garlic, onions, alfalfa, some truck crops, and pasture. Annual rainfall averages <12 cm, the average computed from numerous years without rain interspersed with an occasional heavy downpour.

Ornithologically, the Mulegé region has received only anecdotal attention (Wilbur personal communication, Howell and Webb 1992), even though the area is home to 3 species endemic to BC, Xantus' Hummingbird (nomenclature follows the 1983 AOU Check-list with appropriate supplements; see Appendix for scientific names), Belding's Yellowthroat, and Gray Thrasher. In addition, recent observations indicate that a small colony of Least Grebes breed within the freshwater lagoon at Mulegé (Howell and Webb 1992, personal observation) and large concentrations of Hooded Oriole breed in the palmar.

Field data were collected during February, March, April, and November 1996 and February and March 1997. The data consist of direct observation enhanced with playbacks of recorded songs/calls. Here we summarize new, noteworthy or locale-specific information for 17 species, some of which may be considered common, but for which no Mulegé records are provided in published sources (e.g., Nelson 1921, Grinnell 1928, Wilbur 1987, Howell and Webb 1992, 1995). In addition, we provide tabular summarization of our data for all species observed during the 3 time periods. Precise latitude/longitude locations were determined using GPS (Garmin model #100), while approximate (hereafter approx.) locations were determined from an atlas of surface maps (Topographic International, Inc. 1986).

ANNOTATED SPECIES ACCOUNTS

Least Grebe. Observed at the freshwater oasis each day it was visited. In spring adults were attracted to tape recordings of their advertisement and distress calls. As many as 6 adults could be seen at 1 time within 50 m of the tape player. All birds observed in March were in full adult breeding plumage (red eyes and lack of a white throat). Two juveniles were observed on 26 April 1996. This species was not recorded in brackish water of tidal Rio Mulegé. Based on playbacks, we estimate that there were at least 8 pairs of Least Grebes in the oasis; we know of at least 1 successful nesting attempt. Howell and Webb (1992) also observed them in the oasis and cited 2 other observations, from 1987 and 1988. This species was formerly common in the cape region but has declined in that area because of habitat degradation (Wilbur 1987:32–33). Since this oasis is highly impacted by humans and appears to be degenerating and since this situation is common at most of the other BC oases (Wilbur 1987, Grismer and McGuire 1993), there is little hope for long-term survival of the local population.

Western Grebe. One observed at Estero San Marcus, a saltwater lagoon located approx. 20 km northeast of Mulegé (approx. 27°07′N, 112°04′W). Wilbur (1987:34) lists this species as "occasional" in the Gulf of California while Howell and Webb (1995:97) include it as a nonbreeding (wintering) species "less common" in the gulf than on the Pacific coast. Howell and Webb (1992) provide 5 winter records, 3 of which are from the Pacific coast, 1 from the interior and 1 from the Cape region. The location closest to Mulegé is San Ignacio (approx. 27°17′N, 112°54′W).

White-faced Ibis. On 12 November 1996 we observed 4 individuals feeding in an irrigated alfalfa field about 8 km west of Mulegé. On 15 November 1996 at Rio Mulegé, we observed 4 feeding individuals on exposed mud flats at low tide. It cannot be determined if these 2 sightings were the same individuals. Wilbur (1987:51) lists this species as a rare transient, providing 3 location records: Maneadero (approx. 31°44′N, 116°33′W), La Purísima (approx. 26°12′N, 112°04′W), and 3 records at La Paz (approx. 24°08′N, 110°17′W). An immature was recorded on 11 June 1991 at San José del Cabo (approx. 23°03′N, 109°43′W; Howell and Webb 1992). The range map in Howell and Webb (1995:147) includes all of Baja as transient/wintering range, but the account does not provide documentation for BCS.

Greater White-fronted Goose. On 11 November 1996 nine individuals were in an irrigated alfalfa field approximately 10 km west of Mulegé. They took off, flying due east down the valley toward the town. On 14 November 1996 we observed 9 individuals from close range (<10 m) swimming in the freshwater lagoon at Mulegé. The furthest south for which Wilbur (1987:53) provides documentation is Bahía San Quintín (approx. 30°27′N, 115°57′W) on the Pacific coast. The range map in Howell and Webb (1995:155) shows the transient/winter range of this species only on the Pacific coast side of the peninsula, although the west coast of mainland Mexico is included.

Anna's Hummingbird. We found this species to be common at feeders, with documented sight records continuously from 29 February through early April 1996, when all hummingbird use of feeders diminished. Howell and Webb (1992) report them in October north of Mulegé at Guerrero Negro (approx. 27°58′N, 114°03′W) on the west coast and south at the El Tripui resort south of Loreto (approx. 26°N, 111°27′W) on the east coast. Wilbur (1987:109) reports that the species is an "uncommon resident" south to 30° on the mainland and to 28° on islands. Howell and Webb (1995:425) state that Anna's Hummingbirds winter south to about Guerrero Negro. The maximum number we recorded at any 1 time was 4 individuals (2 males and 2 females on 3 March 1996).

Rufous Hummingbird. For this report we assume that individuals with rufous tails and green backs were Allen's Hummingbirds while those with rufous tails and rufous backs were Rufous Hummingbirds (although this may be unreliable; Phillips 1975, Kaufman 1990). From 1 March through 25 March 1996 they were abundant at feeders, with peak numbers (>7 males and >5 females seen at 1 time) on 3 March. The last individual (1 female) was seen on 25 March. When present, we noted that they dominated all other species at the feeders, including the much larger Xantus' Hummingbird. Howell and Webb (1995:428) do not include this species on their range map for BCS, while Wilbur (1987:109–110) states that it is an ". . . uncommon spring and fall transient the length of the peninsula. . . ." None of Wilbur's documented sites, however, include Mulegé. Phillips (1975) postulates a spring migration route out of the state of Sinaloa into Sonora, Mexico, and across the Sea of Cortez at approximately 30°N. Our data indicate that the crossover is at least 26° and possibly further south.

Allen's Hummingbird. Observed almost daily from 1 March through 13 March 1996, departing nearly 2 wk before the last Rufous Hummingbird. Howell and Webb (1995: 428–429) do not include this species in BCS, while Wilbur (1987:110) lists them as common to abundant transients in ". . . northwestern Baja California . . . ," presumably not BCS. Phillips (1975) summarizes specimen locations for this species, noting only 6 spring specimens, 1 each on 22 February 1925 at Santo Domingo (approx. 30°46′N, 115°57′W on the Pacific coast) and 25 February 1925 at San Quintín (approx. 30°27′N, 115°57′W on the Pacific coast), and 4 on 2 March 1945 at Isla Cedros (a continental island approx. 28°15′N, 115°20′W on the Pacific side). There were no specimen records for BCS and none for mainland Mexico for April and May. Our data support the contention that Allen's Hummingbirds complete their northward migration before Rufous Hummingbirds but not the supposition that they cross the Sea of Cortez at about 30° north.

Costa's Hummingbird. Although it is widely known that this species is the most abundant hummingbird in desert areas of BC, we report 3 unusual nest locations. The 1st site was an active nest with 2 eggs that was constructed on a piece of fishnet material slung under a blue glass fishing float used as a decoration hanging on a patio outside a home. Interestingly, the nest was adorned with pale blue plastic fibers (perhaps from a piñata?) which nearly exactly matched the glass of the float. We discovered the nest when it had 2 eggs, both of which hatched and later fledged. The 2nd and 3rd nests were located under the edge of television satellite dishes adjacent to patios. The contents of the 1st Costa's nest were unknown, but the female was sitting tight from 1 March through 15 March 1996. Its ultimate outcome is likewise unknown. The 2nd nest contained 2 nestlings that were being fed as of 9 March 1997.

Red-breasted Sapsucker. One, an adult male, was observed on 3 consecutive days in early March 1997 in the mixed mesquite/"palmar" habitat edging Rio Mulegé. We place these observations on record, since Wilbur (1987:111–112) states that they are a ". . . sparse winter visitor October to February throughout . . ." BC and provides only Grinnell's (1928) location summaries, none of which is within 250 km of Mulegé.

American Robin. One individual was observed by 3 people over a 2-h period on 15 November 1996 at the Rancho La Ventana, approximately 10 km west of Mulegé in an agricultural area. The bird in question was extremely gray in coloration and was initially identified by us as a female American Robin in basic plumage. However, after examining our field notes, field guide illustrations, several American Robin females collected in Baja or nearby desert locales, and 8 specimens of "San Lucas" Robins collected in Baja, we are left undecided about the positive identification of this bird. The back, wings, nape, crown, and forehead were too gray and the breast and abdomen were not rufous enough for a desert area American Robin female in unworn basic plumage. However, the breast and abdomen were not as "washed out" as a typical "San Lucas" Robin. In either event the record is of note since Wilbur (1987:132) lists American Robins as an ". . . uncommon migrant and winter visitor, chiefly in the north . . ." with supportive sightings including December at Bahía de Los Angeles (approx. 29°N, 113°34′W) and May at La Laguna (approx. 23°06′N, 109°36′W) in the cape region. In addition, he lists the "San Lucas" Robin as native only to the mountains of the cape region. Howell and Webb (1995:592) include similar information from the above locations in their range maps. Neither reference includes the area surrounding Mulegé. In addition, American Robins are listed as breeding in BCN (Howell and Webb 1992). In summary, the individual we observed was more than 200 km south of the published range of the American Robin and more than 300 km north of the range of the "San Lucas" Robin. The plumage did not fit "perfectly" either of the two, but was closer to the latter.

European Starling. During November we observed this species daily in the agricultural valley west of Mulegé. This species was less common in spring of 1996, but during spring 1997 many individuals were observed defending potential hole nest locations amongst the cardón (*Pachycereus*). This is south of previously published winter sightings at Guerrero Negro (approx. 27°58′N, 114°03′W; Wilbur 1987:137, Howell and Webb 1992, 1995:613). This species appears to be continuing its southward colonization route.

Pyrrhuloxia. Observed commonly during spring 1996 and 1997 and fall 1996 in a variety of habitats including backyard feeders, irrigated cropland, open desert and mixed scrub, contrary to Grinnell (1928:184) who confines the species to mesquite (*Prosopis* sp., Mimosoideae) associations. Mulegé is near the northern edge of the year-round range of this and the following species (Wilbur 1987:148, Howell and Webb 1995:682). Supporting spring documentation for Pyrrhuloxia includes "very rare" at Santa Rosalia (approx 27°20′N, 112°16′W, approx. 30 km north of Mulegé), "fairly common" at Santa Aguenda (approx. 27°03′N, 112°25′W, between Santa Rosalia and Mulegé), Bahia Agua Verde (approx. 25°28′N, 111°15′W, south of Loreto), and El Triunfo (approx. 23°45′N, 110°10′W, south of La Paz).

Northern Cardinal. Observed on several dates and at several locations, including 3 March 1996 in mixed shrub habitat, 7 March 1996 at a feeder in the Oasis Rio Mulegé, and captured on 8 March 1997 in a mist net located in desert scrub habitat 10 km west of town. Many of the contour feathers covering the back of this individual were either entirely gray or tipped with gray, typical of desert-dwelling cardinals in basic plumage. This gave a pale cast to the overall ventral appearance. Northern Cardinals are common and widespread south of Santa Rosalía (approx. 27°20′N, 112°16′W; Wilbur 1987:148, Howell and Webb 1995: 681–682), although no records for Mulegé are included.

Clay-colored Sparrow. In November this species was observed on multiple days, often within flocks of Lark Sparrows and Brewer's Sparrows, foraging in the edges of irrigated fields approx. 10 km west of Mulegé. They are "common winter visitors to the Cape District October to April . . . only a few reports north of lat 25° . . ." (Wilbur 1987:153). Documented records include Cataviña (approx. 29°44′N, 114°43′W) and San Ignacio (approx. 27°17′N, 112°54′W). Howell and Webb's (1995:716) range map does not include the Mulegé area.

Song Sparrow. The distribution of this species in central Baja is problematic. Although listed in both Wilbur (1987:157–158) and Howell and Webb (1995:725) as present at the same latitude as Mulegé, the text description in Wilbur lists locations only west of the central mountains, including records from San Ignacio (approx. 27°30′N, 112°50′W) south to Comondú (approx. 26°10′N, 111°40′W; Wilbur 1987). This matches the range map given in Grinnell (1928:176, Figure 13). For latitude 26°–27°N the range map in Howell and Webb identifies the area *east* of the central mountains. Given the species song/call, especially in spring (March/April), it should have been easy to observe. However, we have no records from early spring/late fall 1996, although a single male did respond to a song playback on 2 different days at the freshwater lagoon in early March 1997. Song Sparrows are known from 3 additional areas in BC: northwest coastal mountains south to El Rosario (approx. 30°03′N, 115°44′W), Rio Colorado (exact location unknown but approx. 31°50′N, 114°15′W), and a small population discovered recently in the oasis at Cataviña (approx. 29°44′N, 114°43′W; Howell and Pyle 1990).

Western Meadowlark. This species was heard/seen regularly, March 1996 and 1997 and November 1996, in irrigated alfalfa fields approx. 10 km west of Mulegé. They are known breeders in northwestern BC with winter records south to San Ignacio (approx. 27°20′N, 112°50′W; Wilbur 1987:160–161). Howell and Webb (1992, 1995:738) include all of BCS as winter range and include 1 summer record from Ciudad Insurgentes (approx. 25°10′N, 111°45′W), taking advantage of recent agricultural development.

Brown-headed Cowbird. Although none were observed during spring 1996 or 1997, a small flock (<20 individuals) was observed on 13 November and again on 15 November 1996 foraging in a heavily grazed alfalfa field in the agricultural valley approx. 10 km west of Mulegé. Although the range map in Howell and Webb (1995:742) places the year-round range of this species throughout BC, no documentation is provided. Wilbur (1987:162) lists this species as a regular winter visitor south to the cape district, with 1 supportive record for La Paz (approx. 24°10′N, 110°35′W) in January, but as a breeder only in BCN. Our data support the contention that cowbirds are winter visitants to the Mulegé, not year-round residents.

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APPENDIX

Summary of observational bird data arranged by habitat type. Abundant (A) = seen daily with little or no effort, common (C) = usually seen in appropriate habitat by experienced observer, fairly common (F) = seen more than once in appropriate habitat by experienced observer, uncommon (U) = seen in appropriate habitat by experienced observer looking specifically for that species, rare (R) = seen once in appropriate habitat by experienced observer.

		Habitat type									
		Pelagic and shore		Freshwater lagoon[3]		Saltwater estuary[3]		Irrigated cropland[3]		Sarcocaulescent desert	
Species[1]	Status[2]	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa
Least Grebe *(Tachybaptus dominicus)*	Re			C	C						
Pied-billed Grebe *(Podilymbus podiceps)*	Re			F	F						
Eared Grebe *(Podiceps nigricollis)*	Mi	A	A								
Blue-footed Booby *(Sula nebouxii)*	Re	C	C								
Brown Booby *(Sula leucogaster)*	Re	A	A								
Brown Pelican *(Pelecanus occidentalis)*	Re	A	A								
Double-crested Cormorant *(Phalacrocorax auritus)*	Re	A	A								
Brandt's Cormorant *(Phalacrocorax penicillatus)*	Re	C	C								
Magnificent Frigatebird *(Fregata magnificens)*	Re	A	A								
Great Blue Heron *(Ardea herodias)*	Re			C	C	C	C				
Great Egret *(Casmerodius alba)*	Re			C	C	C	C	C	C		
Snowy Egret *(Egretta thula)*	Re			C	C	C	C	C	C		
Little Blue Heron *(Egretta caerulea)*	Re					F	F				
Tricolored Heron *(Egretta tricolor)*	Re					U	U				
Reddish Egret *(Egretta rufescens)*	Re					F	F				
Cattle Egret *(Bubulcus ibis)*	Re					F	F	F	F		
Green-backed Heron *(Butorides striatus)*	Re			U	U						
Black-crowned Night-Heron *(Nycticorax)*	Un					C	C				
Yellow-crowned Night-Heron *(Nycticorax violacens)*	Un					F	F				
White-faced Ibis *(Plegadis chihi)*	Wi						U		U		
Greater White-fronted Goose *(Anser albifrons)*	Wi				R				R		
Green-winged Teal *(Anas crecca)*	Wi			U	U						
Mallard *(Anas platyrhynchos)*	Wi			F	F	F	F				

		Habitat type									
		Pelagic and shore		Freshwater lagoon[3]		Saltwater estuary[3]		Irrigated cropland[3]		Sarcocaulescent desert	
Species[1]	Status[2]	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa
Northern Pintail *(Anas acuta)*	Wi					C	C				
Blue-winged Teal *(Anas discors)*	Wi					F	F				
Cinnamon Teal *(Anas septentrionalium)*	Wi			U	U						
Gadwall *(Anas strepera)*	Wi			U	U	U	U				
American Wigeon *(Anas americana)*	Wi					C	C				
Redhead *(Aythya collaris)*	Wi				F						
Ring-necked Duck *(Aythya americana)*	Wi			F	F	F	F				
Lesser Scaup *(Aythya affinis)*	Wi			C	C	C	C				
Bufflehead *(Bucephala albeola)*	Wi			F	F						
Ruddy Duck *(Oxyura jamaicensis)*	Re			C	C						
Osprey *(Pandion haliaetus)*	Re	A	A	F	F	A	A				
Cooper's Hawk *(Accipiter cooperi)*	Re							U	U	U	U
Northern Harrier *(Circus cyaneus)*	Re								U		
Harris Hawk *(Parabuteo uncinctus)*	Re										U
Red-tailed Hawk *(Buteo jamaicensis)*	Re							C	C	C	C
American Kestrel *(Falco sparverius)*	Re							C	C	C	C
Merlin *(Falco columbarius)*	Wi								U		
Peregrine Falcon *(Falco peregrinus)*	Re								U		
California Quail *(Callipepla californica)*	Re							A	A	A	A
Sora *(Porzana carolina)*	Re			F	F	U	U				
Common Moorhen *(Gallinula chloropus)*	Re			F	F						
American Coot *(Fulica americana)*	Re			A	A	C	C				
Black-bellied Plover *(Pluvialis squatarola)*	Wi	C	C								
Semipalmated Plover *(Charadrius semipalmatus)*	Wi	F	F								
Killdeer *(Charadrius vociferus)*	Re	C	C					F	F		
Black-necked Stilt *(Himantopus mexicanus)*	Wi	F	F								

		Habitat type									
		Pelagic and shore		Freshwater lagoon[3]		Saltwater estuary[3]		Irrigated cropland[3]		Sarcocaulescent desert	
Species[1]	Status[2]	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa
American Avocet (*Recurvirostra americana*)	Wi	U	U								
Greater Yellowlegs (*Tringa melanoleuca*)	Wi	U	F			U	F				
Solitary Sandpiper (*Tringa solitaria*)	Wi	F				F					
Willet (*Catoptrophorus semipalmatus*)	Wi	C	C			C	C				
Spotted Sandpiper (*Actitis macularia*)	Wi	F	F			F	F				
Whimbrel (*Numenius phaeopus*)	Wi	F	F			F	F				
Long-billed Curlew (*Numenius americanus*)	Wi	F	F			F	F	F	F		
Marbled Godwit (*Limosa fedoa*)	Wi		F				F				
Sanderling (*Calidris alba*)	Wi		U								
Bonaparte's Gull (*Larus philadelphia*)	Wi		A				A				
Heerman's Gull (*Larus heermanni*)	Re	C	C			C	C				
Yellow-footed Gull (*Larus livens*)	Re	C	C			C	C				
Elegant Tern (*Sterna elegans*)	Re	C	F			C	F				
White-winged Dove (*Zenaida asiatica*)	Re	F	F					C	A	C	A
Mourning Dove (*Zenaida macroura*)	Re	U	U					U	U	U	U
Common Ground-Dove (*Columbina passerina*)	Re			F	F	F	F	C	C	F	F
Greater Roadrunner (*Geococcyx californianus*)	Re							F	F	F	F
Great Horned Owl (*Bubo virginianus*)	Re			F	F	F	F	F	F		
Xantus' Hummingbird (*Hylocharis xantusii*)	Re			C	C	C	C	C	C	F	F
Anna's Hummingbird (*Calypte anna*)	Re			F	F	F	F				
Costa's Hummingbird (*Calypte costae*)	Re			A	A	A	A	A	A	A	A
Rufous Hummingbird (*Selasphorus rufus*)	Mi			C		C					
Allen's Hummingbird (*Selasphorus sasin*)	Mi			F		F					
Belted Kingfisher (*Ceryle alcyon*)	Wi					F	F				
Gila Woodpecker (*Melanerpes uropygialis*)	Re			A	A	A	A	C	C	C	C
Red-naped Sapsucker (*Sphyrapicus varius*)	Wi			U							

		Habitat type									
		Pelagic and shore		Freshwater lagoon[3]		Saltwater estuary[3]		Irrigated cropland[3]		Sarcocaulescent desert	
Species[1]	Status[2]	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa
Ladder-backed Woodpecker (*Picoides scalaris*)	Re							F	F	F	F
Gilded Flicker (*Colaptes chrysoides*)	Re							F	F	F	F
Gray Flycatcher (*Empidonax wrightii*)	Wi							U	F	U	F
Black Phoebe (*Sayornis nigricans*)	Wi			C	C						
Say's Phoebe (*Sayornis saya*)	Wi							U	U	U	U
Vermilion Flycatcher (*Pyrocephalus rubinus*)	Re							A	A		
Ash-throated Flycatcher (*Myiarchus cinerascens*)	Re									C	C
Cassin's Kingbird (*Tyrannus vociferans*)	Wi							C	C		
Violet-green Swallow (*Tachycineta thalassina*)	Re			F	F			C	C		
Tree Swallow (*Tachycineta bicolor*)	Wi				C				F		
Western Scrub Jay (*Aphelocoma californica*)	Re							F	F	F	F
Common Raven (*Corvus corax*)	Re							A	A	A	A
Verdin (*Auriparus flaviceps*)	Re			F	F	F	F	C	C	A	A
Cactus Wren (*Campylorhynchus brunneicapillus*)	Re							C	C	C	C
Canyon Wren (*Catherpes mexicanus*)	Re									U	U
Marsh Wren (*Cistothorus palustris*)	Re			C	C						
House Wren (*Troglodytes aedon*)	Re							F	F		
Blue-gray Gnatcatcher (*Polioptila caerulea*)	Re			F	F			C	C		
California Gnatcatcher (*Polioptila californica*)	Re							F	F	A	A
American Robin (*Turdus migratorius*)	Wi								R		
Northern Mockingbird (*Mimus polyglottos*)	Re			F	F	F	F	C	C		
Gray Thrasher (*Toxostoma cinereum*)	Re							U	U	F	F
Phainopepla (*Phainopepla nitens*)	Re			U	U			F	F	F	F
Loggerhead Shrike (*Lanius ludovicianus*)	Re							C	C	F	F
European Starling (*Sturnus vulgaris*)	Re							F	F		

		Habitat type									
		Pelagic and shore		Freshwater lagoon[3]		Saltwater estuary[3]		Irrigated cropland[3]		Sarcocaulescent desert	
Species[1]	Status[2]	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa	Sp	Fa
Yellow-rumped Warbler (*Dendroica coronata*)	Wi			C	C	C	C	C	C		
Belding's Yellowthroat (*Geothlypis beldingi*)	Re			C	C						
Orange-crowned Warbler (*Vermivora celata*)	Wi			F	F	F	F	F	F		
Northern Cardinal (*Cardinalis*)	Re			U	U	U	U	F	F		
Pyrrhuloxia (*Cardinalis sinuatus*)	Re			F	F	F	F	F	F		
Green-tailed Towhee (*Pipilo chlorurus*)	Wi							C	C	F	F
Clay-colored Sparrow (*Spizella pallida*)	Un								U		
Song Sparrow (*Melospiza melodia*)	Un			R							
Brewer's Sparrow (*Spizella breweri*)	Wi							F	F		
Black-chinned Sparrow (*Spizella atrogularis*)	Re								U		
Lark Sparrow (*Chondestes grammacus*)	Wi							A	A		
Black-throated Sparrow (*Amphispiza bilineata*)	Re									C	C
White-crowned Sparrow (*Zonotrichia leucophrys*)	Wi			A	A	A	A	C	C		
Western Meadowlark (*Sturnella neglecta*)	Un							C	C		
Brown-headed Cowbird (*Molothrus ater*)	Un								U		
Hooded Oriole (*Icterus cucullatus*)	Re			A	A	A	A	F	F		
House Finch (*Carpodacus mexicanus*)	Re			C	C	C	C	C	C	F	F
Lesser Goldfinch (*Carduelis psaltria*)	Re							F	F		
House Sparrow (*Passer domesticus*)	Re			A	A	A	A				

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[1] Common and scientific names follow American Ornithologists' Union Check-list of North American Birds (1983) and supplements (1985, 1987, 1989, 1991, 1993, 1995).

[2] Re = year-round resident, Mi = migrant, Wi = winter resident, Un = status uncertain.

[3] Including associated edge habitat within 50 m of water.

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INTERANNUAL ABUNDANCE OF NONNATIVE FATHEAD MINNOWS (*PIMEPHALES PROMELAS*) IN UPPER KLAMATH LAKE, OREGON

David C. Simon[1] and Douglas F. Markle[1]

ABSTRACT.—Since its introduction about 20 yr ago, fathead minnow (*Pimephales promelas*) has become very abundant in Upper Klamath Lake, Oregon. In 1991 mean beach seine catch per unit effort (CPUE) was 214, compared to 25 for native blue chub (*Gila coerulea*), the next most abundant species. In 45 trap-net samples collected in 1992, fathead minnow constituted 59% of the fishes caught in Agency Lake subbasin, 27% in Upper Klamath Lake, and 17% in tributary inflow habitats. From 1991 to 1995 fathead minnow declined and the abundance of some native fishes increased. Introduction to Klamath Basin was coincident with U.S. Environmental Protection Agency promotion of fathead minnow as bioassay subjects. Upper Klamath Lake fathead minnow have incomplete lateral lines and males have mandibular tubercles diagnostic of the northeastern subspecies. Although the origin, as bait bucket transfer, forage fish, or laboratory release, cannot be determined with certainty, the possibility of laboratory release suggests modification of bioassay protocols to require destruction of test or excess subjects.

Key words: fathead minnow, Oregon, nonnative species, species interactions, baitfish introductions, laboratory release.

Fathead minnow (*Pimephales promelas*) is broadly distributed east of the Rocky Mountains with a native range from Great Slave Lake, Canada, to Chihuahua, Mexico, and eastward to the Appalachians (Vandermeer 1966, Lee and Shute 1980). Hubbs and Black (1947) recognized 2 broadly distributed subspecies: *P. p. promelas*, a midwestern to northeastern form with an incomplete lateral line and nuptial tubercles on the lower jaw of breeding males; and *P. p. confertus*, a southwestern form with a complete lateral line and no nuptial tubercles on the lower jaw.

Fathead minnow was first collected from Oregon in Spencer Creek, a small tributary to Klamath River, 27 km downstream of Upper Klamath Lake on 13 May 1974 (Andreasen 1975). First reported in Upper Klamath Lake in 1979 (Ziller 1991), it was occasionally captured there in 1982 by Oregon Department of Fish and Wildlife (ODFW). By 1983 fathead minnow was captured in each ODFW trap net set (J. Ziller, fisheries biologist, ODFW, personal communication), and by 1993 we had captured the species from Klamath Marsh National Wildlife Refuge (50 km northeast of Upper Klamath Lake) and Gerber Reservoir (50 km southeast of Upper Klamath Lake; unpublished data).

Fathead minnow has been introduced in many western states as a bait and forage fish. State-sanctioned propagation and distribution began in adjacent states of Idaho about 1945 (Simpson and Wallace 1978) and California in 1953 (Shapovalov et al. 1959). Published information suggests early introductions of fathead minnow as bait and forage fish were *P. p. confertus*, the southwestern form (Evans and Douglas 1950, Miller 1952, Minckley 1973). The northeastern form of fathead minnow, *P. p. promelas*, was promoted as a bioassay subject by the U.S. Environmental Protection Agency (EPA) beginning in the late 1960s (EPA 1972, Brauhn and Schoettger 1975).

In this paper we document relative abundance of fathead minnow in Upper Klamath Lake from 1991 to 1995, discuss possible impacts on native fish, and compare the fish fauna before and after its introduction. We also comment on diagnostic morphological characters of Upper Klamath Lake fathead minnow and suggest possible origin(s).

DESCRIPTION OF AREA

Upper Klamath Lake, the headwaters of the Klamath River, is in south central Oregon east

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of the Cascades (Fig. 1) at 1262 m; it drains 9415 km^2 of mixed forest, grass-shrub flatland, and marshes (Johnson et al. 1985). The Williamson River is the major tributary, providing about half the inflow, while its northern subbasin, Agency Lake, is fed by the Wood River (Johnson et al. 1985). It is the largest lake in Oregon with a mean summer surface area of 27,811 ha, 141 km of shoreline, and a mean depth of 2.4 m (U.S. Army Corps of Engineers 1978, Johnson et al. 1985). The lake is hypereutrophic, highly turbid, and caustic (pH typically >9.0), with wide diel fluctuations in dissolved oxygen from near depletion to supersaturation (Bortleson and Fretwell 1993). High pH and anoxia are thought to be partially responsible for the declining populations of 2 endangered catostomids, Lost River sucker (*Deltistes luxatus*) and shortnose sucker (*Chasmistes brevirostris;* Scoppettone and Vinyard 1991). A 3rd catostomid in the Klamath Basin, Klamath largescale sucker (*Catostomus snyderi*), was formerly a U.S. Fish and Wildlife Service category 2 candidate species.

SUBSPECIES IDENTIFICATION

We identified the subspecies of fathead minnow in Upper Klamath Lake using criteria of Hubbs and Black (1947): a complete lateral line and absence of mandibular nuptial tubercles on breeding males to diagnose *P. p. confertus*, and an incomplete lateral line and presence of mandibular nuptial tubercles on breeding males to diagnose *P. p. promelas*.

The following museum specimens were examined: Oregon, Klamath Drainage, Oregon State University (OS) 4944, OS 7953, OS 7955, OS 12506, OS 14116, OS 14326, OS 14327; Minnesota, Great Lakes Drainage, OS 14274 (from stocks maintained by EPA Environmental Research Laboratory–Duluth); and New Mexico, Rio Grande Drainage, Museum of Southwestern Biology, University of New Mexico (MSB) MSB 735.

Average lateral line completeness (pored/total lateral line scales) was 41% (range 6–83%, standard deviation [*s*] = 0.18) in Klamath, 41% (7–98%, *s* = 0.29) in Great Lakes and 95% (81–100%, *s* = 0.07) in Rio Grande fathead minnows. Breeding males from Upper Klamath Lake had an average of 4.3 (2–7, *s* = 1.45) tubercles on the chin, Great Lakes specimens had an average of 3.3 (1–5, *s* = 1.41) tubercles, and Rio Grande specimens had no chin tubercles.

Vandermeer (1966) showed a sharp break in lateral line completeness, with populations north and east of Kansas being 2.2–49.9% complete and those to the southwest 63.0–95.0% complete. He considered this northeast vs. southwest pattern to "present a classical pattern of subspecific variation." He also showed that mandibular nuptial tubercles on breeding males were virtually absent south of Kansas and high to the east, with 2 populations around Lake Michigan having mean chin tubercle counts of 4.3 and 11.4 (Vandermeer 1966). Upper Klamath Lake fathead minnows appear to be the northeastern subspecies, *P. p. promelas*, rather than the southwestern form, *P. p. confertus*, but this identification should be considered tentative until the systematics of fathead minnow is better resolved.

METHODS

Beach Seine

Beach seine sampling was conducted in 1991, 1993, and 1995 as part of a long-term sampling program of sucker year class strength. Ten sites in Upper Klamath Lake and 5 in Agency Lake (Fig. 1) were sampled with a 6.1-m-long seine with 4.8-mm bar mesh and a 2 × 2 × 2-m bag. A sampling unit was a 1/4 circle arc that sampled 30 m^2. Sites were sampled weekly from 25 July to 26 September 1991, though the full complement of sites was typically not sampled as we implemented other aspects of our catostomid research. Sites were sampled monthly in July and August 1993, and biweekly in July and August 1995.

Analysis of variance (ANOVA) was used to test for differences in relative abundance among years for fathead minnow, blue chub (*Gila coerulea*), tui chub (*Gila bicolor*), and age-0 sucker (both species) catch per unit effort (CPUE). Because catch data frequency distributions were highly positively skewed, data were $\log_e$-transformed (CPUE+1) to better meet assumptions of normality required for ANOVA. Least significant difference (LSD) test was used on mean $\log_e$ (CPUE+1) values to identify interannual differences in abundance for significant ANOVA models. All analyses were performed using Statgraphics Version 7 (Manuguistics 1993).

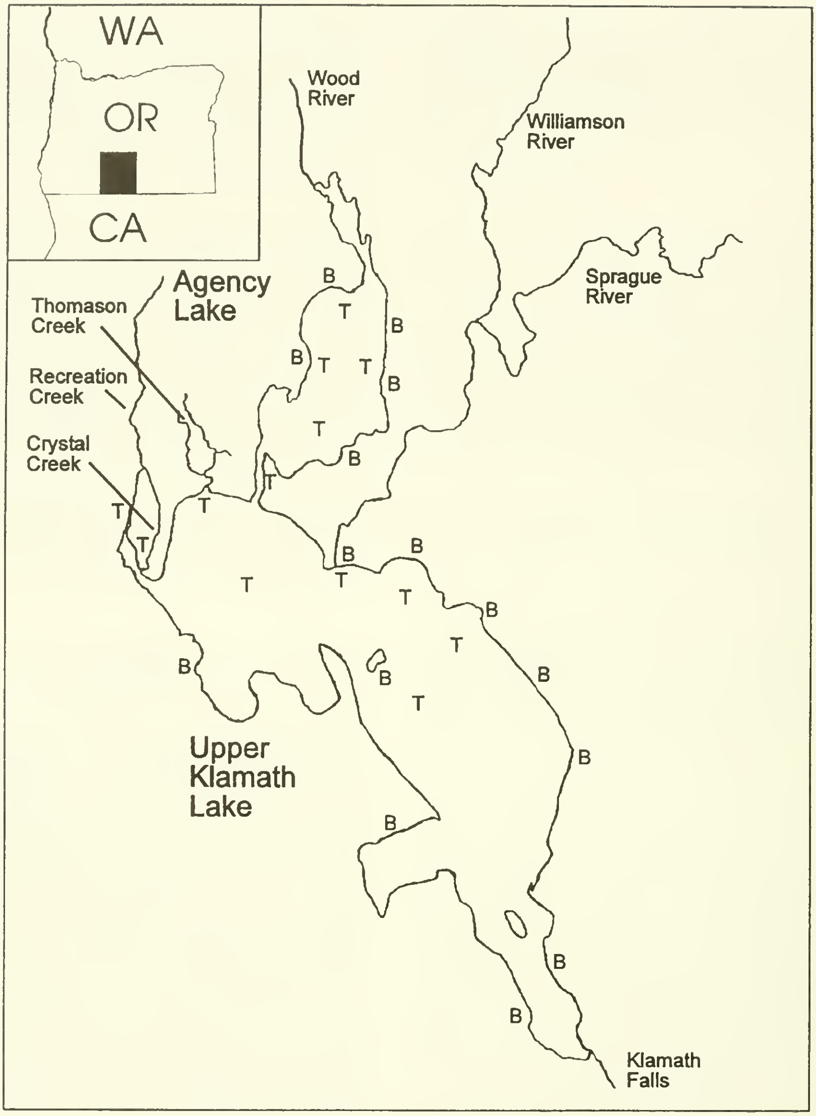
WA
OR
CA
Wood River
Williamson River
Sprague River
Agency Lake
Thomason Creek
Recreation Creek
Crystal Creek
Upper Klamath Lake
Klamath Falls
B
T

Fig. 1. Map showing Upper Klamath Lake and Agency Lake, Oregon. Shoreline beach seine sites are indicated by a B, and trap-net sites are indicated by a T.

Trap Net

Trap-net sampling was conducted from 21 April to 22 October 1992. Sites were in Agency Lake, the northern half of Upper Klamath Lake, and tributary inflows (lower Williamson River, Thomason Creek, Crystal Creek, and Recreation Creek; Fig. 1). Trap nets were 6.5-mm bar mesh, had a single 2.4 × 23-m lead, two 2.4 × 10.7-m wings, and a 1.2 × 1.2-m square frame with two 10-cm throats. Lake trap nets were set offshore in open water. River mouth trap nets were set in mid-channel. Trap nets were usually set overnight and fished for approximately 24 h, but set times ranged from 15.5 to 99.0 h. We found no significant ($P > 0.05$, $r = 0.037$) relationship between number of hours fished and $\log_e$-transformed number of fish caught, so we calculated trap-net CPUE as number per net.

The only available data for evaluating historical change are 1964 and 1965 surveys in Upper Klamath Lake by Vincent (1968). Vincent's data and analyses are difficult to interpret because he reported pooled results from a gang of 3 gill nets and a single hoop net. His gill nets had stretched mesh sizes 32, 45, 57, and 152 mm, but he gave no mesh size for the hoop net. With 1 exception, he reported results as percent composition rather than in terms of effort. We make comparisons of our trap-net data to Vincent's data, but caution that our data are not directly comparable to his, and only crude comparisons are useful.

RESULTS

Beach Seine

Fathead minnow was the most common species in Upper Klamath Lake beach seines during 1991 (CPUE = 214.4, coefficient of variation [CV] = 270), followed by blue chub (CPUE = 24.9, CV = 190) and tui chub (CPUE = 9.6, CV = 266). Fathead minnow density declined significantly ($P < 0.05$) each year from 1991 to 1995, while blue chub and age-0 sucker increased significantly ($P < 0.05$) from 1991 to 1995 (Fig. 2). Tui chub CPUE trended upward each year but was not significant ($P > 0.05$). Except for yellow perch (*Perca flavescens*) in 1993, other species never exceeded 2% of the total catch in any year. Yellow perch was 7% of the 1993 catch, all of which were age-0. Other native species included marbled sculpin (*Cottus klamathensis*), slender sculpin (*Cottus tenuis*), and Klamath Lake sculpin (*Cottus princeps*); nonnative species included yellow perch, bluegill (*Lepomis macrochirus*), and pumpkinseed (*Lepomis gibbosus*).

In Agency Lake beach seine samples, fathead minnow CPUE also decreased significantly ($P < 0.05$) from 1991 (CPUE = 219.6, CV = 179) to 1995 (CPUE = 108.5, CV = 346), with 1993 intermediate (CPUE = 185.8, CV = 161). Changes in abundance of native species were unclear, with no significant ($P > 0.05$) differences among years for blue chub, tui chub, or age-0 sucker CPUE in Agency Lake.

Trap Net

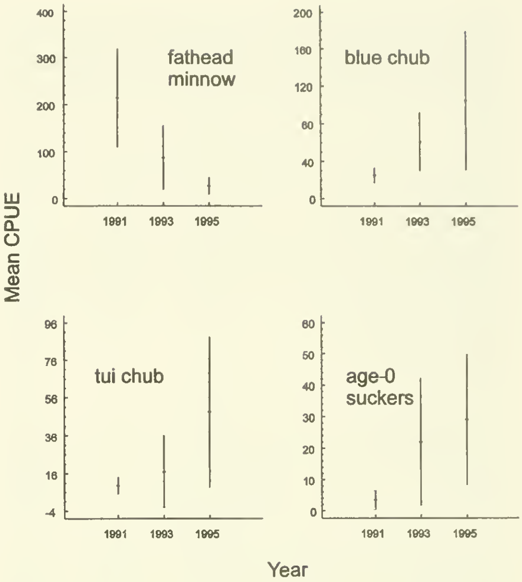

Fig. 2. Mean and 95% confidence intervals of beach seine CPUE for fathead minnow, blue chub, tui chub, and age-0 sucker from Upper Klamath Lake, 1991–1995.

Fish were captured during 45 trap-net samples: 11 from Upper Klamath Lake, 13 from Agency Lake, and 21 from tributary inflow areas. Fathead minnow was the most abundant species captured in Agency Lake, 2nd in abundance in Upper Klamath Lake, and 4th in abundance in tributaries (Table 1). Agency Lake trap nets caught fewer species (10) than Upper Klamath Lake (13) or tributaries (14), but total catch rates were higher. Variation in catch rates was much higher in tributaries than in lake samples (Table 1).

Compared with Vincent's (1968) data, our trap-net data (Table 2) are noteworthy in the presence of fathead minnow. However, without knowledge of the mesh size of Vincent's trap nets, we cannot determine whether fathead minnow were vulnerable to his gear. In our trap nets fathead minnow constituted 17% of the fish in tributaries, 27% in Upper Klamath Lake, and 59% in Agency Lake. Because fathead minnow now represents a substantial portion of the fish fauna, percentages of other species must decline if densities remain constant. Vincent (1968) mentioned tui chub was caught at a maximum rate of about 5 per hour (h) in July and December. Based on his relative species composition (Table 2), Vincent's maximum rate for blue chub must have been about 8.3/h. Our 1992 Upper Klamath Lake trap-net catch rates were 1.1 tui chub/h and 18.9 blue chub/h, indicating that tui chub may have declined after the introduction of fathead minnow. However, we found up to a 5-fold increase in interannual beach seine abundance for tui chub from 1991 (CPUE = 9.6) to 1995 (CPUE = 48.6) and a 4-fold increase in blue chub from 1991 (CPUE = 24.9) to 1995 (CPUE = 105) in our surveys. Thus, apparent changes in abundance from the 1960s in both chub species could be attributed

TABLE 1. Species, mean catch (number per net), median catch (number per net), and coefficient of variation (CV) of the mean for fish caught in trap nets from Upper Klamath Lake, Agency Lake, and tributary inflow habitats in 1992.

Species	Mean	Median	CV
UPPER KLAMATH LAKE			
blue chub	484.1	417.0	88
fathead minnow	175.2	60.0	125
tui chub	41.0	24.0	133
Klamath Lake sculpin	6.5	1.0	175
marbled sculpin	5.7	4.0	144
slender sculpin	1.4	0	244
Pacific lamprey	0.5	0	228
suckers[a]	0.4	0	185
yellow perch	0.1	0	331
brown bullhead	0.1	0	332
pumpkinseed	0.1	0	332
bluegill	0.1	0	332
	715.0	625.0	82
AGENCY LAKE			
fathead minnow	559.8	356.0	109
blue chub	135.5	88.0	104
tui chub	59.2	70.0	77
yellow perch	21.8	0	249
marbled sculpin	2.3	1.0	146
Klamath Lake sculpin	1.3	0	193
Pacific lamprey	1.1	0	180
brown bullhead	0.3	0	205
suckers[b]	0.1	0	361
slender sculpin	0.1	0	361
pumpkinseed	0	0	—
bluegill	0	0	—
	781.5	793.0	81
TRIBUTARY INFLOW HABITATS			
blue chub	105.8	13.0	237
brown bullhead	39.0	0	309
tui chub	17.4	7.0	203
fathead minnow	9.6	3.0	149
yellow perch	4.6	2.0	128
marbled sculpin	3.8	1.0	154
suckers[c]	2.8	1.0	206
Klamath Lake sculpin	2.5	0	201
pumpkinseed	1.0	0	199
Pacific lamprey	0.7	0	183
slender sculpin	<0.1	0	458
bluegill	<0.1	0	458
	187.3	97.0	168

[a] Lost River and shortnose sucker

[b] Lost River sucker

[c] Lost River, shortnose, and Klamath largescale sucker

to fathead minnow introduction, natural population variation, or susceptibility to poorer water quality (Castleberry and Cech 1993).

DISCUSSION

With the possible exception of native catostomids, the fish community of Upper Klamath Lake appears resilient. Williams (1988) partly attributed the decline of Lost River and shortnose suckers to competition and/or predation by nonnative species. Most nonnative species in Upper Klamath Lake (bluegill, pumpkinseed, yellow perch, and brown bullhead [*Ameirus nebulosus*]) are relatively rare, and density-dependent impacts on suckers might be small. However, fathead minnow is still abundant even after a 5-yr decline. Although the fathead minnow reportedly consumes algae, higher plants, zooplankton, and insects (Becker 1983), Dunsmoor (1993) has experimental evidence that it feeds on sucker larvae in aquaria; additionally, Franzin and Harbicht (1992) found walleye (*Stizostedion vitreum*) larvae in fathead minnow stomachs from a Manitoba irrigation drainage.

TABLE 2. Comparison of percent species composition for 1992 trap-net samples from this study with data reported from Upper Klamath Lake by Vincent (1968): UKL = Upper Klamath Lake, AL = Agency Lake, and TI = tributary inflow habitats.

Species or species group	TI	AL	UKL	Vincent (1968)
lampreys	2	<1	<1	<1
trouts	—	—	—	<1
brown bullhead	13	<1	<1	5
tui chub	10	9	7	35
blue chub	36	20	62	58
fathead minnow	17	59	27	—
suckers	1	<1	<1	<1
sculpins	13	2	4	<1
yellow perch	8	9	<1	2
sunfish	<1	—	<1	<1

If fathead minnow has a density-dependent impact on suckers or other native fishes, we might expect a compensatory response to the fathead minnow decline we observed from 1991 to 1995. Extraneous mechanisms influencing the direction of change of fish abundances from 1991 to 1995 are unknown. Because Upper Klamath Lake is managed by the U.S. Bureau of Reclamation as an irrigation reservoir, lake levels are regulated. However, there is no active management to reduce fathead minnow abundance. Only 2 active management strategies have been implemented as a consequence of endangered species listing of Lost River and shortnose sucker: (1) closure of a snag fishery on adult sucker, and (2) prolonged elevation of springtime water levels. The 1st strategy would seem to have little impact on fathead minnow abundance. The 2nd inundates sucker spawning gravels and shoreline vegetation and was designed to provide cover to reduce larval sucker vulnerability to predation. However, prolonged springtime water levels could also promote fathead minnow abundance by providing complex structural spawning habitat, such as undersurfaces of rocks, logs, and vegetation (Scott and Crossman 1973, Becker 1983). Although the trends evident in Figure 2 suggest that elevated springtime water levels had the desired effect by increasing young sucker abundance, they did not increase fathead abundance.

Native fishes have responded positively to declines of nonnatives in other systems, such as the Great Lakes (Jude and Tesar 1985, Eck and Wells 1987), North Carolina streams (Lemly 1985), and Great Smoky Mountains National Park streams (Moore et al. 1984). However, we found no documentation of responses of western U.S. native fishes where spread of nonnatives has seriously compromised many native fish populations (Minckley and Douglas 1991, Rinne and Minckley 1991). We have demonstrated in Upper Klamath Lake that decreasing abundance of nonnative fathead minnow is associated with increasing abundance of some native fishes.

Finally, diagnostic characteristics of Klamath fathead minnows indicate they are of northeast origin, possibly including the Great Lakes region where EPA began use and promotion of fathead minnow as a standard bioassay subject. Governmental and other laboratories using fathead minnow in bioassay work, as well as baitshops, obtain supplies from multiple sources, often the lowest bidder. Thus, it is not known whether there have been laboratory releases of fathead minnow and, if so, whether these could be distinguished from baitfish release. However, their detection in Oregon was coincident with the promotion of fathead minnow by EPA and 21–29 yr after their introduction as baitfish in neighboring Idaho and California (Shapovalov et al. 1959, Simpson and Wallace 1978).

The potential for nonnative bioassay subjects to be released—and the irony that it might happen in the furtherance of environmental protection—suggests a prudent countermeasure. Although the EPA's published protocols specify initial quarantine of incoming fish, they do not specify disposition of excess or test fathead minnow except in some larval assays where specimen fixation in formalin is part of the assay (Brauhn and Schoettger 1975, Norberg and Mount 1985, DeGraeve et al. 1991). It can be argued that states govern access, distribution, and handling of fishes within their borders; but a laboratory's record for following EPA protocols may be a greater incentive than poorly enforced state regulations, and the costs of disastrous introductions far outweigh the minimal costs associated with destruction of test organisms. All protocols for bioassay of exotic organisms should specify destruction of all test and all excess individuals at the end of the bioassay.

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WINTER HABITAT SELECTION BY REINTRODUCED PRONGHORN ON ANTELOPE ISLAND, GREAT SALT LAKE, UTAH

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ABSTRACT.—The recent and future introduction of several ungulate species on Antelope Island necessitates knowledge of habitat use by each species. In this study habitat preferences of reintroduced pronghorn (*Antilocapra americana*) on Antelope Island were evaluated during February–March 1993 and January–March 1994. Elevation, slope, physiography, aspect, and habitat type of sites used by pronghorn were compared to similar data collected from random points. During the severe winter of 1993, pronghorn preferred terrain that was 1281–1380 m in elevation and was relatively flat or at the base of a hill. Slopes greater than 30% were avoided. South-facing slopes were preferred; west-facing slopes were avoided. Pronghorn preferred sagebrush habitats and avoided grasslands. During the mild winter of 1994, pronghorn showed preferences for slightly higher elevations, avoided slopes greater than 30%, but used other habitat features in proportion to their availability. Future winter studies of pronghorn should include considerations of snowfall patterns and the availability, versus the abundance, of sagebrush.

Key words: pronghorn, antelope, Antilocapra americana, *habitat selection, winter habitat, habitat availability.*

With the introduction of pronghorn into new areas, many questions must be answered concerning their winter habitat preferences. Factors such as vegetation availability and diversity, snow depth, and physiography may play an important role in their survival. Past habitat studies have considered these factors, but many neglected to examine a particular feature's availability when results were interpreted (but see Amstrup 1978, Clary and Beale 1983, Ryder and Irwin 1987). Availability is important because observed habitat use by pronghorn may simply reflect the occurrence of habitat types in the area. Only when animals use certain features out of proportion to their availability can they be said to prefer or avoid those features (Marcum and Loftsgaarden 1980).

Optimal winter habitat with ample vegetation is critical for pronghorn survival. A severe winter with heavy snowfall and low temperatures can result in higher mortality from malnutrition (Martinka 1967, Van Wormer 1969) and may lead to a low production of young the following spring (Martinka 1967). Additionally, deep snow can hinder winter movements by pronghorn (Van Wormer 1969, Mitchell 1980, Kindschy et al. 1982), affect vegetation availability (Hovey and Harestad 1992), and increase predation risk (Van Wormer 1969).

The reintroduction of pronghorn onto Antelope Island State Park in the Great Salt Lake, Utah, provided an excellent opportunity to study winter habitat selection of pronghorn. The recent and future introduction of other ungulates on the island necessitates knowledge of critical pronghorn winter habitat to minimize potential interspecific competition. Identification of these critical areas also can be used in planning construction of hiking and bike trails to avoid human use of prime winter habitat. The objective of this study was to determine which factors affect winter habitat preferences of pronghorn and thus to provide data for better management of pronghorn on Antelope Island.

STUDY AREA

Antelope Island State Park, in the southeastern region of the Great Salt Lake, is about 16 km from Salt Lake City, Utah (Fig. 1). The island was closed to the public from 1983 to 1993 because of rising lake levels that flooded the 11.6-km causeway leading to the island.

The 10,409-ha island is topographically diverse, ranging in elevation from 1280 to 2011 m (Jones 1985, Utah Department of Natural Resources 1988). Average annual precipitation is 43 cm, with 10.8 cm falling January–March (National Weather Service Forecast Office [NWSFO], Salt Lake City International Airport, Salt Lake City, Utah). Most of the island

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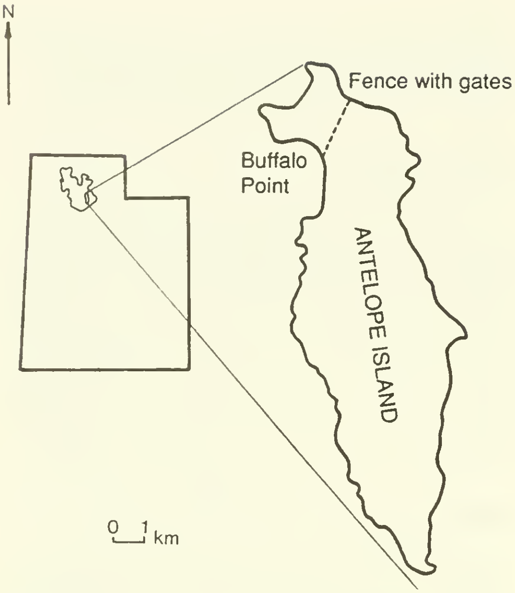

Fig. 1. Antelope Island State Park study area in the Great Salt Lake, Utah. Pronghorn moved from north to south through several open gates along the fence on the north side of the island.

is grassland with patches of sagebrush (*Artemisia* spp.) and a few small riparian and marsh areas. Intermittent streams run on the island in spring and summer seasons. Average temperatures for January, February, and March of 1993 were –3.9°C, –1.4°C, and 7.5°C, respectively; snowfall was 127.8 cm in January, 33.5 cm in February, and a trace in March. For winter 1994, temperatures averaged 2.7°C in January, 1.8°C in February, and 7.6°C in March; snowfall was 15.7 cm, 38.1 cm, and 7.9 cm, respectively (NWSFO).

Antelope Island was named by John C. Fremont in the 1840s for the herds of pronghorn inhabiting it. However, the last pronghorn on the island was sighted in 1870 (M. A. Larsson personal communication). The island also is inhabited by about 500 bison (*Bison bison*) and 70 mule deer (*Odocoileus hemionus*), with populations of coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and Golden Eagles (*Aquila chrysaetos*) as potential predators of pronghorn.

MATERIALS AND METHODS

Twenty-three pronghorn were captured with a net-gun in Summit County, Utah, and released on Antelope Island 30 January 1993. Three bucks from Morgan County, Utah, introduced to the island in May 1993, and 10 fawns born in May and June 1993 were included with the original 23 pronghorn in the 1994 field season. Prior to release onto the island, each animal was fitted with a solar-powered radio transmitter (Advanced Telemetry Systems, Inc., Box 398, Isanti, MN 55040) mounted on a standard livestock ear tag.

Pronghorn were tracked February–March 1993 and January–March 1994 in all weather conditions, using radiotelemetry to locate groups. Data were collected 2–3 d per week between 0700 and 1800 h. No animal was included in more than 1 group on the same day, and groups were noted as separate only if they were separated by ≥0.5 km. Pronghorn observations stopped when winter groups began to disperse and bucks began establishing territories (31 March 1993 and 20 March 1994).

The visual location of each group was marked on a topographic map. Dominant vegetation, physiography, and elevation were noted. Later the site was revisited to measure slope, using a clinometer, and aspect (north 315–44°, east 45–134°, south 135–224°, or west 225–314°). Slope was categorized into 2 groups (<30% and >30%) because slopes >30% were scarce; this also facilitated comparison with previous studies (Kindschy et al. 1978).

Categorization of physiography and vegetation type occupied was subjective but consistent. We categorized the physiography of each point as relatively flat (little or no slope), slope of hill, top of hill, base of hill, or terrace. Dominant vegetation was categorized as grassland (few or no sagebrush, bushes, or trees), sagebrush (some grass and forbs), sagebrush-dunes (sand dunes where sagebrush predominates), or shrub (woody vegetation other than sagebrush). We used only grassland and sagebrush habitats in the statistical analysis due to limited availability of other vegetation types, even when all other types were combined into a single group.

Air temperature at the time of the sighting of each pronghorn group was recorded. Snow depth at the site was recorded by relating the depth of snow to the length of the pronghorn's hind legs. Wind direction and velocity data were obtained from the closest weather station to the island, the Salt Lake International Airport (NWSFO), about 26 km southeast of Antelope Island. Wind conditions at the weather station and on the island were comparable as both occur on the valley floor equidistance from the mountain range. Readings are taken hourly at the station, and we used values closest to the times of pronghorn group sightings.

Sites used by pronghorn were compared to 76 randomly selected sites to determine habitat preferences. We determined the number of random sites by estimating that 20 sightings of pronghorn groups would be made per month over the 2-winter study period. When determining random-point distribution, we considered the whole island because it was impossible to define a priori the boundaries of available range.

Random points were chosen using a random-number table and a grid (60 × 60 m) superimposed onto a 7.5-minute series topographic map. Once the location in the field was approached as closely as possible with a topographic map, we selected the exact spot for data collection by releasing a rock on a string that had been swung overhead. At each of these random points, the elevation, slope, aspect, dominant vegetation, and physiography were recorded.

Availability of habitat features, as determined by random-point data, was compared to actual pronghorn sightings with chi-square analysis to determine if pronghorn were using a site in proportion to its availability (use = availability; α of 0.05) or not in proportion to availability (use < or > availability). If pronghorn used a habitat less than expected, they were avoiding the feature; if the habitat was used more than expected, the pronghorn were choosing the feature. Following a significant difference as indicated by chi-square, we analyzed elevation, physiography, slope, dominant vegetation, and aspect data with Bonferroni Z tests to determine which categories of each feature were used significantly more or less than expected based on availability (Marcum and Loftsgaarden 1980). In all Bonferroni Z tests, 97% confidence intervals were used for individual categories, and simultaneous α varied with the number of categories in the analyzed feature.

Wind velocity and current temperature each were compared to physiography data and analyzed using the Kruskal-Wallis test to determine if pronghorn use of physiographic features was related to weather conditions. To test whether pronghorn were likely to use certain aspects more than others when wind velocities were high, we calculated median wind velocities for pronghorn observations at different aspects using Kruskal-Wallis. Aspect groups were combined into north- and east-facing and south- and west-facing due to small numbers of pronghorn observations at each aspect; north- and east-facing aspects were grouped because these slopes are usually colder than south- and west-facing aspects, on which snow melts more quickly. Snow depth in areas used by pronghorn was summarized but not analyzed statistically because availability data were collected in the summer.

RESULTS

In winter 1993, 47 observations of pronghorn groups were made; each group consisted of 2–23 pronghorn (mean ± s = 14 ± 8 animals). Forty pronghorn groups were observed in winter 1994; groups consisted of 1–36 pronghorn (mean ± s = 11 ± 11 animals).

Snowfall was heavy during 1993, totaling 161.3 cm in January and February (NWSFO). By 6 March snow was patchy, and by 15 March it remained only at higher elevations. Snow depth at the sites where pronghorn were observed ranged from 0 to 10 cm. Pronghorn were found in areas free of snow 48% of the time and in areas with snow 52% of the time (n = 21 observations of groups). Snowfall on the island was minimal during winter 1994, a total of 61.7 cm in January, February, and March (NWSFO). When snow did fall, it melted within 1–2 d. Consequently, pronghorn were observed in snow only 4 times.

During 1993 pronghorn groups occupied sagebrush habitats in greater proportion than their availability, and grasslands less than their availability (Fig. 2A; $\chi^2 = 4.3$, df = 1, $P < 0.05$). In contrast, no preferences were observed in pronghorn use of vegetation types during 1994 ($\chi^2 = 2.1$, df = 1, $P > 0.05$).

During winter 1993 pronghorn preferred elevations of 1281–1380 m and avoided those from 1481 to 1880 m (Fig. 2B; $\chi^2 = 15.8$, df = 3, $P < 0.01$). During 1994 pronghorn preferred elevations of 1381–1480 m and avoided all higher elevations ($\chi^2 = 9.8$, df = 3, $P < 0.05$). During 1993 pronghorn groups used south-facing aspects in greater proportion than their availability and west-facing aspects less than their availability (Fig. 2C; $\chi^2 = 9.6$, df = 3, $P < 0.05$). Pronghorn groups showed no preferences or avoidances in use of aspect during

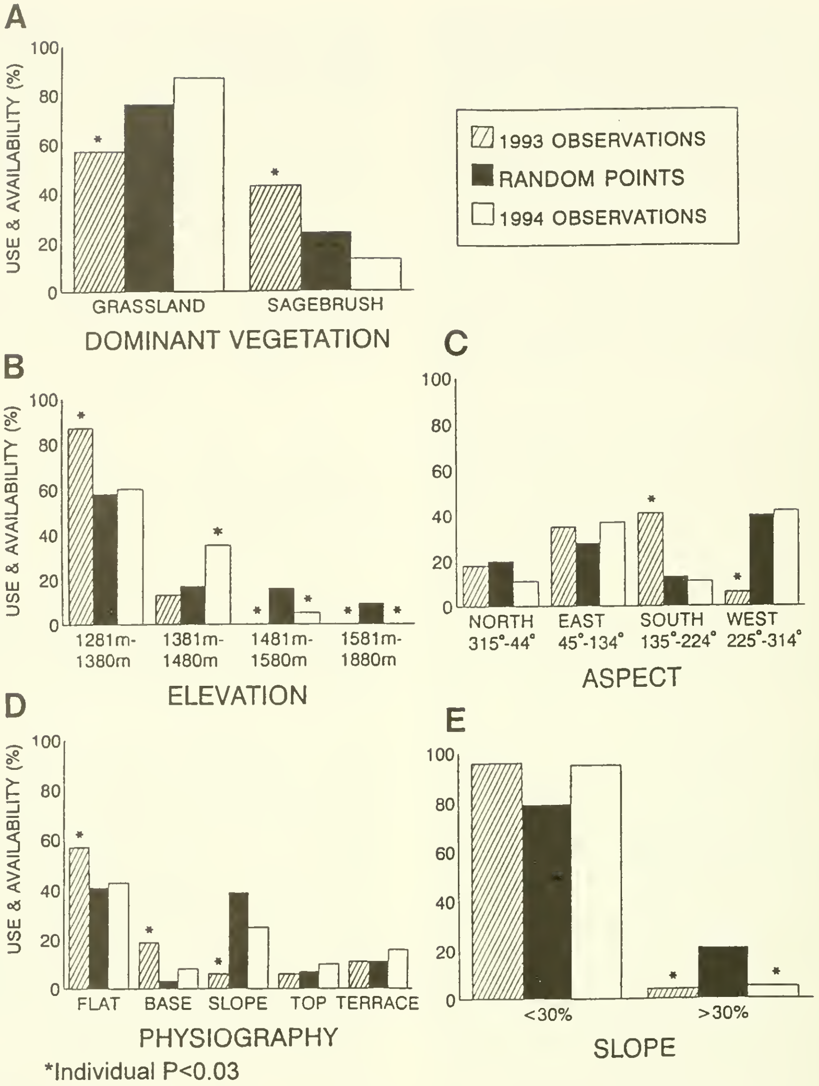

Fig. 2. Use versus availability of habitat characteristics by pronghorn on Antelope Island, Great Salt Lake, Utah, during the winters of 1993 and 1994. Use refers to pronghorn observations. Availability refers to collected random-point data; 1993: $n = 47$ observations, 1994: $n = 40$ observations.

the winter of 1994 ($\chi^2 = 1.1$, df = 3, $P > 0.05$).

Relatively flat areas and bases of hills were used during 1993 in greater proportion than their availability; slopes of hills were avoided (Fig. 2D; $\chi^2 = 22.4$, df= 4, $P < 0.01$). In contrast, pronghorn groups exhibited no preferences or avoidances of physiographic features during the winter of 1994 ($\chi^2 = 4.0$, df = 4, $P > 0.05$). Pronghorn groups avoided slopes >30% during the winters of 1993 (Fig. 2E; $\chi^2 = 6.6$, df = 1, $P < 0.02$) and 1994 ($\chi^2 = 5.1$, df = 1, $P < 0.05$). During both 1993 and 1994, current temperature and pronghorn use of physiographic features were not related (1993: $H = 5.93$, df = 4, $P > 0.05$; 1994: $H = 3.84$, df = 4, $P > 0.05$), nor was the use of physiographic features related to wind velocity (1993: $H = 4.33$, df = 4, $P > 0.05$; 1994: $H = 4.57$, df = 4, $P > 0.05$). Wind velocity during 1993 was not correlated with aspects of terrain used by pronghorn ($H = 0.59$, df = 1, $P > 0.05$); however, during the winter of 1994 pronghorn use of north and east aspects was associated with higher wind velocities ($H = 4.17$, df = 1, $P < 0.05$). The median and modal wind direction was 150° (i.e., from the southeast); therefore, use of north and east aspects was probably not due to thermoregulatory constraints.

DISCUSSION

Pronghorn exhibited more habitat preferences and avoidances during winter 1993 than 1994 due to heavy snowfall that limited vegetation availability. Use of the lowest elevations and relatively flat areas during 1993 may have aided pronghorn in predator avoidance and detection (Van Wormer 1969, Bruns 1977, Vaughan 1986). Pronghorn use of slopes <30% was consistent both years and with previous studies (Amstrup 1978, Kindschy et al. 1978) and also may reflect predator-avoidance behaviors; however, we have no direct evidence to support or refute this explanation, as there was no winter mortality despite frequent sightings of coyotes in the area.

Particularly during a severe winter, snow depth can affect the amount of forage available for ungulate consumption (Hovey and Harestad 1992). Pronghorn apparently preferred sagebrush habitats in 1993 because grassland areas were buried in deep snow. Pronghorn in Alberta were seen pawing through snow to reach food, even when other vegetation was available above the snow (O'Gara 1978), but we did not observe that behavior in this study. Additionally, higher concentrations of fats and proteins in sagebrush than in cured grasses may make sagebrush a preferred winter forage (Martinka 1967, Sundstrom et al. 1973); but the absence of habitat preferences in 1994, when there was little snow, suggests accessibility was the main preference factor.

Pronghorn preference for south-facing aspects may be related to their release near an east-west ridge known as Buffalo Point (Fig. 1). The severe winter, deep snow, and uncertainty of being in a new habitat could have caused the animals to remain in this location where sagebrush was readily available on a south-facing slope. However, their preference for south-facing aspects during winter 1993 was consistent with previous studies (Clary and Beale 1983); the warmer aspects provide faster snowmelt, thus increasing food availability.

On 4 August 1994 most of Buffalo Point burned, including almost all of the sagebrush. Few other areas on Antelope Island have south-facing aspects and sagebrush for pronghorn survival during a severe winter (Moss and Vaughn 1996). Future plans for the island should include habitat restoration with the planting of sagebrush on south-facing aspects. Additionally, studies that incorporate the Geographic Information System (GIS) with habitat preferences of all park ungulates would be beneficial in planning the development of trail systems and other human uses on the island (e.g., Koeln et al. 1994, Lachowski et al. 1994, Bosakowski et al. 1995, Moss and Vaughn in press).

As many as 15 mule deer and 100 bison were seen in the vicinity of pronghorn during winter. In addition, bighorn sheep (*Ovis canadensis*) are to be introduced to the state park in January–March 1997. Thus, competition for food and space may be an important consideration, especially during severe winters. Pronghorn appear to graze compatibly with bison, deer, and bighorn sheep (Yoakum 1980), and in some areas, mule deer and pronghorn have little overlap in habitat use during winter (Wood 1989). However, with few sagebrush areas, limited space, and increasing ungulate populations on the island, it is critical to continue to monitor habitat use to examine future competition for food and space.

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CLASSIFICATION AND ORDINATION OF *COLEOGYNE* COMMUNITIES IN SOUTHERN NEVADA

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ABSTRACT.—Woody plant community composition was analyzed throughout the range of *Coleogyne ramosissima* in the Spring and Sheep Mountain ranges of southern Nevada. The lower *Coleogyne* elevational boundary was analyzed in detail in Lucky Strike Canyon, on the eastern edge of the Spring Mountains. TWINSPAN (2-way indicator species analysis) identified 4 primary species and stand groups from the 2 mountain ranges (extensive survey), and 4 primary species and stand groups in the detailed study at the lower *Coleogyne* ecotone (intensive survey). Analysis of DECORANA (detrended correspondence analysis) results indicated that elevation and soil depth were the environmental factors most significantly associated with distribution of species and stand groups in the extensive survey. Elevation was the only significant physical factor associated with distribution of species and stand groups in the intensive survey. Five vegetation zones from the 2 mountain ranges were identified based on their dominant species in 15 extensive transects. *Coleogyne* were subdivided into pure stands and upper and lower ecotones for further investigation of species distribution and environmental factors. Selected environmental factors appear to play an important role in structuring the Mojave Desert vegetation zones in southern Nevada.

Key words: Coleogyne ramosissima *Torr., classification, ordination, vegetation zones, Lucky Strike Canyon, Spring Mountains, Sheep Range.*

Three dominant vegetation types characterize southern Nevada: *Larrea tridentata* Cov.–*Ambrosia dumosa* Payne (valley floors and lower mountain slopes), *Coleogyne ramosissima* Torr. (mid-elevation slopes), and *Pinus monophylla* Torr. & Frem.–*Juniperus osteosperma* Little (upper elevation slopes). The *Coleogyne* vegetation zone, ranging from 1200 to 1550 m in elevation in southern Nevada, is characterized by a closely spaced matrix of *Coleogyne* with a scattered distribution of other shrub species. Previous studies have shown that air temperatures in the *Coleogyne* community in Utah range from –24° to 47°C (Korthuis 1988). Korthuis (1988) proposed that the upper limit of *Coleogyne* distribution may be set by low air temperatures and that cold air draining from adjacent mountain slopes may limit *Coleogyne* establishment on basin floors. Alternatively, the lower limit of *Coleogyne* may be determined by low soil moisture in Utah (Bowns 1973). Annual precipitation ranging from 180 to over 270 mm appears to be required for development of *Coleogyne* stands in the Mojave Desert (Hunter and McAuliffe 1994). Shallow soils are typical of *Coleogyne* communities and may partially determine its abundance and distribution in Utah (Callison and Brotherson 1985). Distribution of *Coleogyne* in Utah may thus depend largely upon abiotic factors. However, little is known about the factors that determine the pattern of *Coleogyne* distribution in southern Nevada.

In this study we determined the spatial arrangement of *Larrea-Ambrosia*, *Coleogyne*, and *Pinus-Juniperus* vegetation along an elevational gradient and the percent cover for all woody perennial species. We also classified vegetation using TWINSPAN and determined the relationship between the distribution of desert plant species groups and environmental factors based on correlations with axis values from DECORANA.

STUDY AREA

This study was located in the Spring (36°0′N, 115°30′W) and Sheep (35°50′N, 115°35′W) Mountain ranges, approximately 65 km northwest of Las Vegas, Nevada. Precipitation patterns of southern Nevada include summer storms and winter rains. Summer storms generally occur in July and August and can sometimes be local and intense. Winter rain is widespread and may last up to several days. Snow is frequent at high elevations, particularly in the *Pinus-Juniperus*

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woodlands and upper *Coleogyne* ecotones. Precipitation is positively correlated with increase in elevation (Rowlands et al. 1977).

Southern Nevada is an area of temperature extremes, with a mean minimum winter temperature of –10°C and summer temperatures of above 47°C. Temperature means and extremes are negatively correlated with increasing elevation (Rowlands et al. 1977). Relative humidity is low (≤ 20% is common in the summer months), resulting in exceedingly high evaporation.

METHODS

Broad patterns of vegetation zonation were examined with 12 elevational transects located on the Spring Mountains and 3 on the Sheep Range in summer 1993. The transects contained 9–16 circular (100-m^2, 5.65-m radius) plots spaced at a fixed elevational interval of 65 m. Average number of plots per transect was 12. Transects were located east, west, and south of the Spring Mountains and east and west of the Sheep Range. Each transect included 2 plots in the *Larrea-Ambrosia* shrubland just below the *Coleogyne* shrubland (mean elevation 1155 ± 40 m; Lei and Walker 1997), extended throughout the entire *Coleogyne* zone (mean elevation 1560 ± 45 m; Lei and Walker 1997), and included 2 plots in the *Pinus-Juniperus* woodland just above the *Coleogyne* zone (mean elevation 1870 ± 50 m; Lei and Walker 1997).

A portion of the lower ecotonal area of *Coleogyne* was examined in detail at the location of one of the original transects on the eastern side of the Spring Mountains. Six replicate 100-m^2 circular plots were located at each of 6 elevations at 30-m elevational intervals in Lucky Strike Canyon between 1160 and 1310 m elevation. The lowest elevation included 6 plots just below the lower elevational limit of *Coleogyne*. The remaining 5 elevations represented increasing levels of *Coleogyne* density, but the *Coleogyne* shrubland extends to 1600 m in Lucky Strike Canyon (Lei and Walker 1997). Data collected in these "intensive" plots were also collected in the "extensive" plots that covered the entire elevational range of *Coleogyne*.

Within each plot we recorded the presence of all woody perennial species (>10 cm tall), including subshrubs. Subshrubs are plants that have suffrutescent stems at the base with herbaceous stems making up the canopy. Canopy diameters were calculated by computing the average of the longest and shortest dimension of the plant cover. Elevation and aspect of each plot were measured. We visually estimated percentage of rock, soil, and vegetation cover and assigned each plot to 1 of 6 cover categories (absent, 1–5%, 6–25%, 26–50%, 51–75%, and 76–100%). We classified topography of each plot as slope, terrace, or dry wash, repositioning when cliffs, rocky areas, and streambeds were encountered. New plots were positioned horizontally approximately 20 m from the transect at an identical elevation to avoid these habitats. Ground surface was characterized as desert pavement, loose rocks, sand, and sand with boulders.

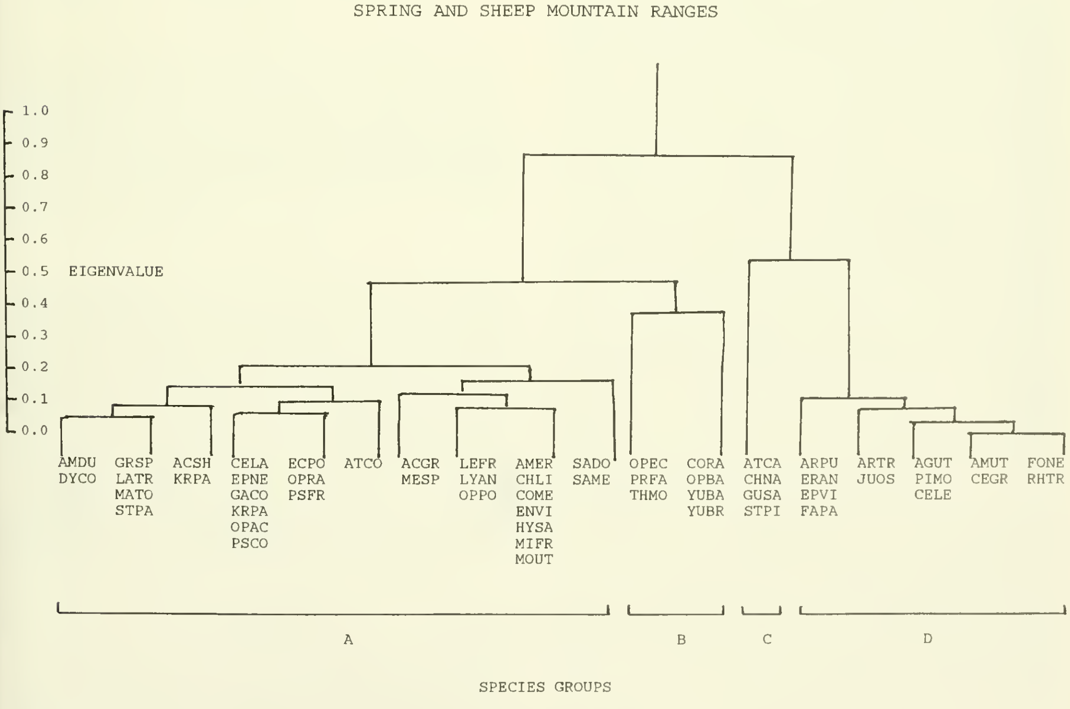
Using TWINSPAN (Hill 1979a), we classified sampled plots into vegetation types and generated groups of species based on vegetation similarities among the sampled stands. Each stand group represented a vegetation zone from the lowest to the highest elevational groups in the part of the Spring and Sheep Mountain ranges sampled. Stand group 1 was characterized by *Larrea-Ambrosia* shrublands, while stand group 4 was characterized by *Pinus-Juniperus* woodlands. Using TWINSPAN analysis, we divided the sampled plots into 2 groups, each of which was then divided again, and so on. The dichotomy was terminated if there were 4 or fewer plots in a group (Kent and Coker 1992). Kent and Coker (1992) further proposed that the size of the eigenvalue generated at each dichotomy by TWINSPAN analysis reflects the importance of each component in explaining the total variation within the data set. The eigenvalue, ranging from 0 to 1, was largest at the initial dichotomy and became smaller with each successive dichotomy. One sampled plot from Red Rock Canyon of the Spring Mountains was eliminated due to the existence of numerous rare (riparian) species.

We used DECORANA (Hill 1979b) to generate species and stand ordination scores. These scores were based on the percent cover value of each woody species. Each point on the diagram corresponds to a species, and distances between points on the graph are approximations of their degree of similarity (Kent and Coker 1992). Distances between points on the diagram increased as species distributions diverged and as species occupied different vegetation zones. Similarly, stand ordination scores were also generated by DECORANA, and the interpretation resembled species ordination scores. Distances between points increased as stand distributions diverged. Stand scores could be matched with several environmental variables to detect vegetation and plot variation in relation to the environment. Environmental variables used in our study included elevation, topography, soil depth, plot aspect, type of ground surface, and percent soil and rock cover. Stand aspect could not be correlated because all stands occurred on northwest-facing slopes in Lucky Strike Canyon. Similarily, percent rock cover could not be correlated because all stands had a rock cover of over 75%. The 1st and 2nd ordination axes were orthogonal and indicative of different sources of environmental variation.

Classification and ordination techniques were applied to a total of 180 sampled plots on the 15 elevational transects from the Spring and Sheep Mountain ranges (extensive plots) and 36 plots at the lower elevational limit of *Coleogyne* in Lucky Strike Canyon (intensive plots).

Results

Four major species groups from the 56 woody taxa were identified by TWINSPAN analysis for the extensive transects in the Spring and Sheep mountains (Fig. 1). Species in group A are typical of *Larrea-Ambrosia* stands found at the lower limit of *Coleogyne*; they include *Larrea tridentata*, *Ambrosia dumosa*, *Ephedra nevadensis*, *Yucca schidigera*, and *Acamptopappus shockleyi*. These species tend to occupy slopes and terraces at low elevations. Species in group B are typical of nearly monospecific stands of *Coleogyne* and include *Yucca brevifolia*, *Prunus fasiculata*, and *Thamnosma montana*. Species in group C, typical of the upper *Coleogyne* ecotone, are represented by *Atriplex canescens*, *Gutierrezia sarothrae*, and *Chrysothamnus nauseosus*. Although *Gutierrezia sarothrae* exists in *Coleogyne* stands, it is particularly abundant at the upper *Coleogyne* ecotone. Species in group D are found in the pure *Pinus-Juniperus* woodlands, with *Artemisia tridentata* as the major understory species. *Pinus-Juniperus* are the 2


SPRING AND SHEEP MOUNTAIN RANGES
1.0
0.9
0.8
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EIGENVALUE
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0.1
0.0
AMDU DYCO
GRSP LATR MATO STPA
ACSH KRPA
CELA EPNE GACO KRPA OPAC PSCO
ECPO OPRA PSFR
ATCO
ACGR MESP
LEFR LYAN OPPO
AMER CHLI COME ENVI HYSA MIFR MOUT
SADO SAME
OPEC PRFA THMO
CORA OPBA YUBA YUBR
ATCA CHNA GUSA STPI
ARPU ERAN EPVI FAPA
ARTR JUOS
AGUT PIMO CELE
AMUT CEGR
FONE RHTR
A
B
C
D
SPECIES GROUPS

Fig. 1. Dendrogram of species groups identified by TWINSPAN from 15 elevational transects in the Spring and Sheep Mountain ranges. Main groups were arranged by elevation from the lowest (group A) to the highest (group D). Species are arranged alphabetically within groups. See Appendix 1 for species abbreviations.

co-dominant genera in these woodlands, with *Juniperus osteosperma* more abundant at lower elevations and *Pinus monophylla* at higher elevations. Associated species including *Fallugia paradoxa*, *Ephedra viridis*, *Cercocarpus ledifolius*, and *Forsellesia nevadensis* are also present, but with significantly fewer individuals.

Four main species groups from 26 woody taxa were identified by TWINSPAN analysis for the intensive plots at the lower boundary of the *Coleogyne* shrubland in Lucky Strike Canyon (Fig. 2). Species in group A are typical of *Larrea-Ambrosia* stands dominated by *Larrea tridentata* and *Yucca schidigera*. Species in group B, typical of the lower half of the lower *Coleogyne* ecotone and dominated by *Ambrosia dumosa*, are generally short shrubs. Species in group C are typical of the upper half of the lower ecotone, with *Yucca brevifolia* and *Acamptopappus shockleyi* as the most abundant species. Species in group D are typical of the nearly monospecific *Coleogyne* stands, with *Coleogyne* as the dominant species and *Grayia spinosa* as a common associated species. *Hymenoclea salsola* exists in or near the edges of washes within the *Coleogyne*-dominated stands in this group.

Analysis of the 180 extensive and 36 intensive plots using DECORANA resulted in significant segregation of stand groups from TWINSPAN along axis 1, but not along axis 2 (Fig. 3A). Pearsons correlation analysis indicated that axis 1 of the stand ordination is significantly correlated ($P < 0.001$) with elevation, soil depth, topography, and percent soil cover in the Spring and Sheep Mountain ranges (Table 1). Axis 2 is significantly correlated with elevation, topography, and type of ground surface (Table 1). In Lucky Strike Canyon both axis 1 ($r = 0.90$, $P < 0.001$) and axis 2 ($r = 0.40$, $P < 0.001$) of the stand ordination are significantly correlated with elevation (Table 2). DECORANA also showed a significant stand group segregation along axis 1, but not along

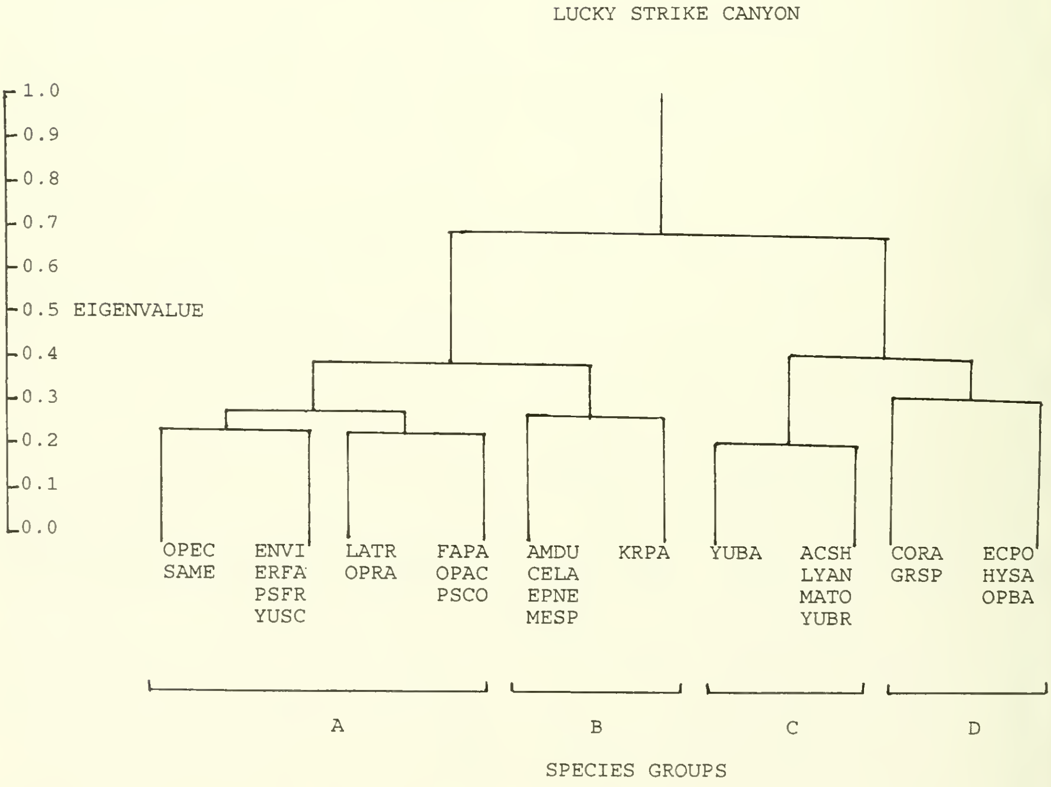

Fig. 2. Dendrogram of species groups identified by TWINSPAN from 6 elevations throughout the lower *Coleogyne* ecotone in Lucky Strike Canyon. Major groups were arranged by elevation from the lowest (group A) to the highest (group D). Species are arranged alphabetically within groups. See Appendix 1 for species abbreviations.

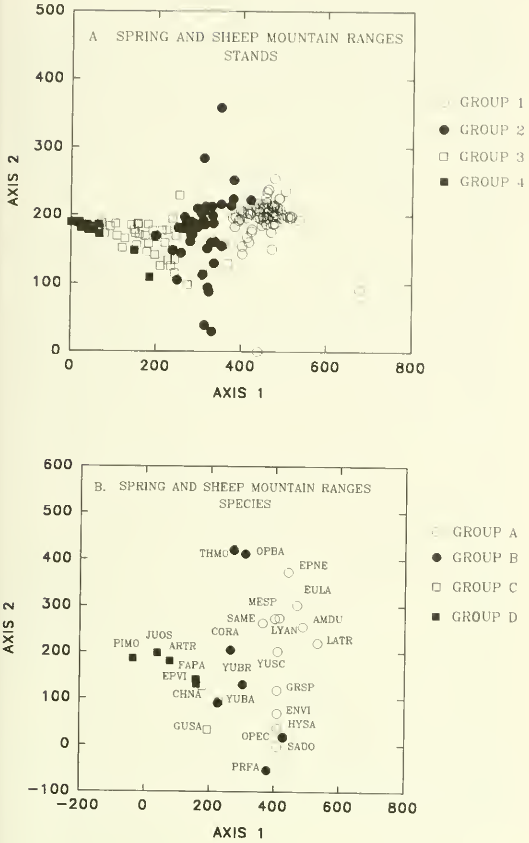

Fig. 3. Ordination of stand (A) and species (B) groups determined by TWINSPAN from the Spring and Sheep Mountain ranges across the entire elevational range of *Coleogyne*. Some uncommon species and overlapping points were eliminated for ease of interpretation and visualization in the species ordination diagram. See Appendix 1 for species abbreviations.

axis 2 in Lucky Strike Canyon (Fig. 4A). Correlations of stand groups vary with each environmental factor. Figures 3B and 4B illustrate the distribution of TWINSPAN species groups and individual species along DECORANA axes 1 and 2 in the Spring and Sheep Mountain ranges and Lucky Strike Canyon, respectively, reflecting differences in the occurrence of various plant species over different elevations and vegetation zones sampled in southern Nevada.

DISCUSSION

Four major species groups that were dominated by *Ambrosia dumosa*, *Coleogyne ramosissima*, *Gutierrezia sarothrae*, and *Pinus monophylla*, respectively, were found to be distributed along gradients determined by elevation and soil depth in the Spring and Sheep Mountain ranges. Four major species groups were also distributed along the lower *Coleogyne* ecotone in Lucky Strike Canyon and were dominated by *Larrea tridentata*, *Ambrosia dumosa*, *Yucca brevifolia*, and *Coleogyne ramosissima*, respectively, determined by elevation.

TABLE 1. Results of Pearsons correlation analysis by matching the 1st and 2nd axis of stand ordination scores acquired from DECORANA to various physical factors in the Spring and Sheep Mountain ranges (Fig. 1A). *r* is the coefficient of linear correlation.

Factor	1st axis	2nd axis
Elevation	−0.79***	−0.21***
Soil depth	−0.54***	-0.03^{NS}
Percent soil cover	−0.35***	-0.10^{NS}
Topography	−0.33***	−0.24**
Ground surface	0.10^{NS}	-0.20^{NS}
Plot aspect	0.10^{NS}	0.03^{NS}
Percent rock cover	0.03^{NS}	0.10^{NS}

**$P < 0.01$
***$P < 0.001$
NS = nonsignificant

In southern Nevada, *Coleogyne* shrublands establish at mid-elevations with well-drained colluvial slopes between elevations of 1300 and 2100 m. *Coleogyne* stands rarely establish above 2000 m unless they are situated on south-facing slopes; *Coleogyne* sometimes establishes below 1300 m on north-facing slopes (Lei and Walker 1997). Callison and Brotherson (1985) noted that *Coleogyne* is the most abundant species in its community and may contribute over 75% of the total vegetation cover, while associated species may contribute less than 15%. Our data confirmed that the *Coleogyne* plant community is nearly monospecific, with other species comprising less than 28% of the total number of species among the 15 transects on 2 mountain ranges. Our data show that *Coleogyne* is a dominant shrub in its vegetation type in terms of height and cover. Many shrub species occur around the periphery of *Coleogyne* canopies because *Coleogyne* roots do not release chemical toxins to repress the growth and development of other nearby species (Bowns and West 1976), which is in contrast to *Larrea* roots (Mahall and Callaway 1992). Cacti are sparsely distributed in the *Coleogyne* shrublands; many cacti are vulnerable to prolonged winter freezing temperatures (Larson 1977). The greatest woody plant diversity is found in or near edges of washes within the *Larrea-Ambrosia* community and the lower *Coleogyne* community.

TABLE 2. Results of Pearsons correlation analysis by matching the 1st and 2nd axis of stand ordination scores acquired from DECORANA to various physical factors in the lower *Coleogyne* elevational boundary at Lucky Strike Canyon (Fig. 2A). *r* is the coefficient of linear correlation.

Factor	1st axis	2nd axis
Elevation	0.90^{***}	0.40^{*}
Ground surface	-0.28^{NS}	0.26^{NS}
Percent soil cover	0.24^{NS}	-0.28^{NS}
Soil depth	-0.17^{NS}	0.03^{NS}
Topography	-0.003^{NS}	0.33^{NS}
Plot aspect	—	—
Percent rock cover	—	—

$^{*}P < 0.05$
$^{***}P < 0.001$
NS = nonsignificant
— = coefficient cannot be computed and correlated

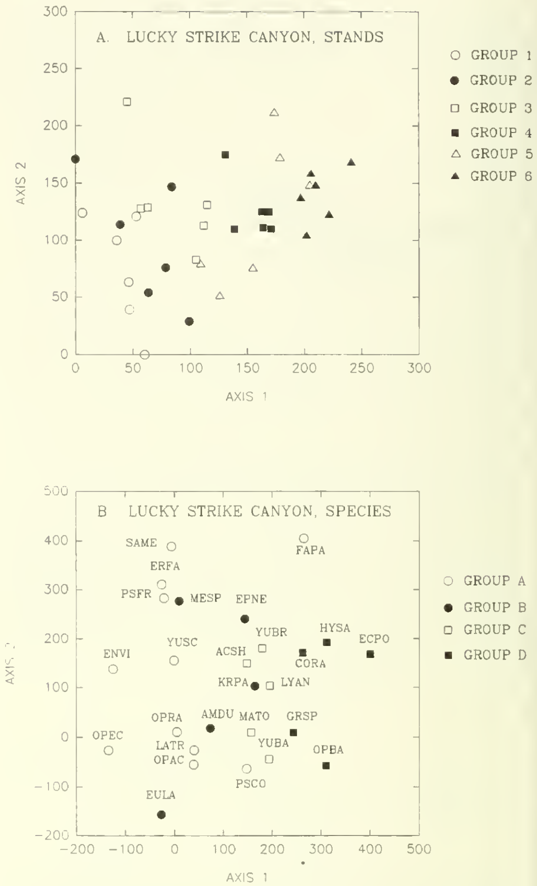

Fig. 4. Ordination of stand (A) and species (B) groups determined by TWINSPAN along the lower *Coleogyne* boundary in Lucky Strike Canyon across the lower ecotone of *Coleogyne*. See Appendix 1 for species abbreviations.

The lower *Coleogyne* boundary generally contains relatively high species richness. This vegetation zone consists of floras from both *Larrea-Ambrosia* and *Coleogyne* shrublands. Such floras include *Yucca schidigera* and *Krameria parvifolia* from *Larrea-Ambrosia* shrublands and *Y. brevifolia* and *Grayia spinosa* from *Coleogyne* shrublands. Species commonly associated with *Coleogyne* begin to establish as elevation increases along the ecotone. A significant overlap of species exists presumably due to the relatively uniform habitat and topography throughout the lower ecotone in Lucky Strike Canyon and on the 2 mountain ranges. Increasing species diversity may partially relate to increases in soil moisture and soil organic matter and to decreases in soil compaction and soil temperatures in Lucky Strike Canyon (Lei and Walker 1997).

Coleogyne gradually becomes less abundant as elevation increases, and it disappears rapidly when *Artemisia tridentata* appears. Harsh and prolonged cold winter air temperatures appear to play a major role in preventing the desert shrubs on lower mountain slopes from migrating upslope. Bowns (1973) proposed that cold air temperatures in winter months may be a factor limiting the distribution of *Coleogyne* at its upper elevational boundary.

A negative correlation exists between the abundance of grasses and shrubs in *Coleogyne* vegetation zones. Grasses, forbs, and cryptogamic crusts are more common on deeper soils where clay, silt, and mineral nutrients are more abundant, and shrubs are more common on shallow and sandy soils (Callison and Brotherson 1985). For these reasons, edaphic factors largely control the distribution of shrubs, grasses, forbs, and cryptogamic crusts in the *Coleogyne* zones. Moreover, West (1983) stated that composition and productivity of annuals in *Coleogyne* communities vary from year to year because they rely heavily on the amount of precipitation. *Bromus rubens* and *B. tectorum* are the primary winter ephemerals. They tend to form carpetlike vegetation among shrubs in the spring seasons during wet years. Although there is a zone of overlap between the 2 *Bromus* species, *B. rubens* is more abundant at the lower *Coleogyne* ecotone, while *B. tectorum* is more common at the upper ecotone (Beatley 1976).

DECORANA analysis of axis 1 of stand ordination reveals significant correlations between the distribution of sample stands and elevation and soil depth in the Spring and Sheep

Mountain ranges (extensive survey). Decreased air and soil temperatures, increased precipitation, and increased soil moisture are associated with increases in elevation for the extensive transects. Factors such as topography and percent soil cover show significant, but weak, correlations with stand ordination scores, indicating some influence of these parameters on the final groupings of stand and species identified by TWINSPAN analysis. Soil depth is a significant physical factor limiting *Coleogyne* distribution. *Coleogyne* communities exhibit relatively shallow soil depth due to caliche layers 30–50 cm beneath the soil surface (West 1983). The area 0–10 cm below the soil surface contains few *Coleogyne* roots; only roots of annuals were identified in this zone (Bowns and West 1976). Shrubs can trap aeolian materials, and greater root activity and weathering cause a depression of the petrocalcic layer directly under shrubs (West 1983). Root biomass is primarily located between 10 and 30 cm and is negatively correlated with soil depth in *Coleogyne* communities (Bowns and West 1976). Soil depth is shallowest in *Coleogyne* communities but deepest in *Pinus-Juniperus* woodlands. Shallow soils result in low root:shoot ratio and limited root development in the *Coleogyne* communities (West 1983).

DECORANA results of axis 1 of stand ordination scores showed a significant correlation between the distribution of sample plots and elevation at the lower *Coleogyne* ecotone of Lucky Strike Canyon. DECORANA axis 2 did not correlate significantly with any physical factors except elevation. Habitat and topography did not change significantly to enhance heterogeneous environmental conditions throughout the lower *Coleogyne* elevational boundary. Hence, elevation is the most essential independent variable to detect stand and species groupings on axis 1 in Lucky Strike Canyon and the Spring and Sheep Mountain ranges in southern Nevada (Tables 1, 2).

Certain physical factors appear to play an essential role in limiting *Coleogyne* distribution to a well-defined elevational band between approximately 1050 and 2150 m in the Spring and Sheep Mountain ranges near Las Vegas, Nevada. Studying an elevational gradient analysis of the Mojave Desert plant communities would contribute to an understanding of which physical factors are most important in determining the current distribution of *Coleogyne* and in structuring vegetation zones in southern Nevada. Relationships between the distribution of sample stands and various physical factors are purely correlative. Experimental, functional, and ecosystem approaches are required to further understand relationships between distributions of plant communities and environmental factors in southern Nevada. Moreover, extensive studies of these physical factors in *Coleogyne* shrublands across its entire geographical range in the southwestern deserts are required to determine ecological requirements of *Coleogyne* and the specific environment it occupies.

ACKNOWLEDGMENTS

We express our gratitude to Yin-Chin Lei and Steven Lei for collecting vegetation and environmental data. Anna Sala assisted with the multivariate analyses (TWINSPAN and DECORANA). We also thank the Motor Pool and Department of Biological Sciences of the University of Nevada–Las Vegas for providing logistical support.

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APPENDIX 1

List of woody perennial species (with abbreviations) found on 15 elevational transects from the *Larrea-Ambrosia* shrublands to the *Pinus-Juniperus* woodlands in the Spring and Sheep Mountain ranges, and on the 6 elevations across the lower *Coleogyne* boundary in Lucky Strike Canyon. Symbols of lifeforms: T = tree, S = shrub, Ss = subshrub, Su = succulent.

Species	Lifeform	Abbreviation
Acacia greggii Gray	T	ACGR
Acamptopappus shockleyi Gray	S	ACSH
Agave utahensis Gray	S	AGUT
Ambrosia dumosa Gray	S	AMDU
Ambrosia eriocentra Gray	S	AMER
Amelanchier utahensis Koehne	T	AMUT
Arctostaphylos pungens HBK	S	ARPU
Artemisia tridentata Gray	S	ARTR
Atriplex canescens Pursh	S	ATCA
Atriplex confertifolia Wats.	S	ATCO
Ceanothus greggii Gray	S	CEGR
Ceratoides lanata Pursh	S	CELA
Cercocarpus ledifolius Nutt.	T	CELE
Chilopsis linearis Cav.	T	CHLI
Chrysothamnus nauseosus Pall.	S	CHNA
Coleogyne ramosissima Torr.	S	CORA
Cowania mexicana Torr.	S	COME
Dyssodia cooperi Gray	S	DYCO
Echinocactus polycephalus Eng. & Big.	Su	ECPO
Encelia virginensis Blake	S	ENVI
Ephedra nevadensis Wats.	S	EPNE
Ephedra viridis Cov.	S	EPVI
Eriodictyon angustifolium Nutt.	S	ERAN
Eriogonum fasciculatum Benth.	S	ERFA
Fallugia paradoxa Endl.	S	FAPA
Forsellesia nevadensis Gray	S	FONE
Gaura coccinea Nutt.	S	GACO
Grayia spinosa Hook.	S	GRSP
Gutierrezia sarothrae Pursh	Ss	GUSA
Hymenoclea salsola T. & G.	S	HYSA
Juniperus osteosperma Torr.	T	JUOS
Krameria parvifolia Benth.	S	KRPA
Larrea tridentata Cov.	S	LATR
Lepidium fremontii Wats.	S	LEFR
Lycium andersonii Gray	S	LYAN
Machaeranthera tortifolia Gray	S	MATO
Menodora spinescens Gray	S	MESP
Mirabilis froebelii Behr.	S	MIFR
Mortonia utahensis Cov.	S	MOUT
Opuntia acanthocarpa Engelm. & Bigel.	S	OPAC
Opuntia basilaris Engelm. & Bigel.	S	OPBA
Opuntia echinocarpa Engelm. & Bigel.	Su	OPEC
Opuntia polyacantha Engelm. & Bigel.	Su	OPPO
Opuntia ramosissima Engelm. & Bigel.	Su	OPRA
Pinus monophylla Torr. & Frem.	T	PIMO
Prunus fasciculata Wats.	S	PRFA
Psilostrophe cooperi Gray	S	PSCO
Psorothamnus fremontii	S	PSFR
Rhus trilobata Nutt.	S	RHTR
Salazaria mexicana Torr.	S	SAME
Salvia dorrii Kell.	S	SADO
Stanleya pinnata Pursh	Ss	STPI
Stephanomeria pauciflora Torr.	S	STPA
Thamnosma montana Torr. & Frem.	S	THMO
Yucca baccata Torr.	S	YUBA
Yucca brevifolia Engelm.	T	YUBR
Yucca schidigera Roezl.	S	YUSC

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BIOTIC AND ABIOTIC FACTORS INFLUENCING THE DISTRIBUTION OF *COLEOGYNE* COMMUNITIES IN SOUTHERN NEVADA

Simon A. Lei[1] and Lawrence R. Walker[1]

ABSTRACT.—*Coleogyne ramosissima* is a desert shrub that forms a nearly monospecific shrubland and occupies a well-defined elevational band between approximately 1050 and 2150 m on mountain ranges in southern Nevada. The *Coleogyne* shrubland shares relatively broad upper and lower ecotones with *Pinus-Juniperus* and *Larrea-Ambrosia* plant communities, respectively. We characterized the extent that environmental factors correlate with *Coleogyne* density and examined variation in biotic and abiotic factors along the lower elevational boundary of *Coleogyne* in Lucky Strike Canyon near Las Vegas, Nevada. *Coleogyne* density was positively correlated with gravimetric soil moisture, soil organic matter, *Coleogyne* water potential, *Coleogyne* stem and leaf phosphorus, and *Coleogyne* leaf biomass. However, *Coleogyne* density was negatively correlated with soil temperatures, soil compaction, and *Coleogyne* stem and leaf nitrogen. *Coleogyne* stem biomass and elongation were generally negatively correlated with *Coleogyne* density. *Coleogyne* density was weakly correlated with soil pH, soil depth, soil nitrogen, soil and leaf phosphorus; these variables did not exhibit a consistent pattern with increasing elevation. Edaphic factors, particularly soil moisture and soil organic matter, appear to play a major role in determining the distribution of *Coleogyne* shrublands in southern Nevada.

Key words: Coleogyne ramosissima, *soils, lower* Coleogyne *ecotone, Lucky Strike Canyon, Mojave Desert.*

Coleogyne ramosissima Torr. (blackbrush) is a member of the Rosaceae family and is the only species in the genus *Coleogyne*. *Coleogyne* primarily establishes along the upper and central portions of the Colorado River drainage and is an endemic yet widespread species in the southwestern United States (Bowns 1973). Previous studies have shown that *Larrea tridentata–Ambrosia dumosa* plant communities appear to dominate between 900 and 1200 m elevation and are replaced by *Coleogyne* communities from 1200 to 1500 m elevation in the Mojave Desert (Beatley 1969, 1976). *Coleogyne* communities are replaced by *Pinus monophylla–Juniperus osteosperma* woodlands at elevations of 1500–1800 m. *Coleogyne* forms nearly monospecific stands in much of its range with relatively broad upper and lower ecotones that overlap adjacent communities by as much as ≥ 100 m in elevation in southern Nevada (Lei and Walker 1995). *Coleogyne* generally grows well on sand, sandy loam, and loam, less well on gravel and clay loam, and poorly on dense clay (Korthuis 1988). A negative correlation exists between the abundance of grasses and shrubs within the *Coleogyne* shrublands. For instance, grasses, forbs, and cryptogamic crusts are more common on deeper soils where clay, silt, and mineral nutrients are more abundant (Callison and Brotherson 1985). Shrubs, on the other hand, are more common on shallow and sandy soils. Bowns (1973) suggested that low soil moisture limits the lower elevational boundary of *Coleogyne* communities in Utah. Hunter and McAuliffe (1994) proposed that an increase in precipitation is the paramount factor permitting the downslope establishment of *Coleogyne*. In the vicinity of Searchlight in southern Nevada, *Coleogyne* establishes as low as 1080 m, whereas around Death Valley of southern California, *Coleogyne* is absent below elevations of 1350 m (Hunter and McAuliffe 1994). Current geographic variation in precipitation appears to control the *Coleogyne* distribution at its lower elevational boundary. We examined abiotic factors that might limit *Coleogyne* at its lower elevational limit in southern Nevada.

HISTORICAL BIOGEOGRAPHY

Packrat (*Neotoma* spp.) midden records from the state of Nevada reveal that woodland vegetation persisted to the end of the early Holocene at elevations as low as 1250 m in the Mojave Desert (Betancourt et al. 1990). As annual temperatures rose, *Pinus-Juniperus*

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trees migrated to higher elevations on desert mountain slopes and were replaced by desert shrubs (Betancourt et al. 1990). *Coleogyne* first appears in the fossil record in 3 late-Wisconsin *Neotoma* deposits in the Frenchman Flat area of southern Nevada (approximately 10,000 yr ago) and should have extended then to about 700 m (Wells and Berger 1967). The entire *Coleogyne* zone and at least the upper part of the *Larrea-Ambrosia* zone around Frenchman Flat were occupied by evergreen *Juniperus* woodlands during the late Pleistocene (Wells and Jorgensen 1964). The arrival of xerophytic shrubs and the extinction of woodlands in low elevations in the Mojave Desert occurred about 8000 yr ago, and vegetation zones migrated upslope significantly around 1000 yr ago and continue through the present time (Betancourt et al. 1990).

Coleogyne can be regarded as a paleoendemic species, exhibiting little variability and perhaps on its way to extinction (Bowns 1973). The shrubs are considered relict because they were probably once more widespread than at present, and their current distribution represents a restriction in their range with time (Bowns 1973). However, paleoecological evidence reveals the *Larrea-Coleogyne* ecotone has undergone frequent elevational migrations during the Quaternary period (Pendleton et al. 1995). Evidence from packrat middens also shows *Coleogyne* has repeatedly moved up and down elevational gradients in response to climatic shifts (Phillips and Van Devender 1974, Cole and Webb 1985, Pendleton et al. 1995). Pendleton et al. (1995) hypothesize that *Coleogyne* is currently migrating into areas where it is adapted to edaphic and climatic conditions. *Coleogyne* shrublands appear to be migrating toward higher elevations on desert mountain slopes in southern Nevada and northward into southern parts of the Great Basin Desert (B. Pendleton personal communication 1994). The ecology of *Coleogyne* seedlings at higher elevations of the Mojave Desert and in the Great Basin Desert may have different dynamics than lower elevation populations in the Mojave Desert. A global climatic shift toward lowered annual precipitation and more extreme fluctuations of temperature and rainfall began in the Tertiary and continued through the Quaternary to the present (Bowns 1973). The current composition and distribution of plant communities in southern Nevada has developed since the last pluvial period (20,000–10,000 yr B.P.; Bradley 1964).

Coleogyne shrublands generally share relatively broad lower ecotones with *Larrea-Ambrosia* in southern Nevada (Lei and Walker 1995). Lucky Strike Canyon represents the typical vegetation and landscape conditions prevailing in the region. The aim of this study was to determine the elevational range and *Coleogyne* density at its lower ecotone. This study also involved an investigation of biotic and abiotic factors along the lower *Coleogyne* elevational boundary in Lucky Strike Canyon.

STUDY AREA

Lucky Strike Canyon is located approximately 65 km northwest of Las Vegas (36°10′N, 115°10′W) between Lee and Kyle canyons on the east-facing slopes of the Spring Mountains in southern Nevada. The *Coleogyne* community in Lucky Strike Canyon is characterized by hot summers above 40°C and cold winters below –10°C. Temperature means and extremes are negatively correlated with elevation. Summer rainfall usually occurs during thunderstorms in July and August and comes from the Gulf of California, drawn into the desert by strong convectional currents (Rowlands et al. 1977). Summer storms are often local and intense. Winter rains, on the contrary, are mild and widespread and come from the Pacific Ocean. They may last up to several days. Snow is frequent at high elevations in southern Nevada, particularly at the upper *Coleogyne* ecotone with *Pinus-Juniperus* woodlands. A relative humidity of ≤ 20% is common in summer seasons. High evaporation and low precipitation create a typical arid environment with an average annual rainfall of <200 mm.

METHODS

Measurements were made in 1993 and 1994 across the lower ecotone of *Coleogyne* in Lucky Strike Canyon. We established six 100-m^2 circular plots (5.65-m radius) along a transect in the center of Lucky Strike Canyon at each of 6 elevations (1160–1310 m; 2.9 km in distance) at 30-m intervals for a total range of 150 m in elevation and a total of 36 plots across the lower *Coleogyne* ecotone. The lowest of the 6 elevations represents *Larrea-Ambrosia* stands, below the range of *Coleogyne* shrubs. The remaining elevations represent increasing levels of *Coleogyne* density, but the *Coleogyne* community extends to over 1600 m elevation in Lucky Strike Canyon (Lei and Walker 1995).

Soil samples at 2 depths (0–7 and 7–15 cm) were collected from random locations within each of the 36 plots with core widths of 12 cm. All soils were passed through a 2-mm sieve before analysis. Soil and air temperatures and soil moisture were measured every 6 wk from May to August 1993; soil moisture was also measured every 6 wk from May to August 1994. We took soil temperature readings using a soil thermometer with the probe at the soil surface and at 5, 10, and 15 cm below the surface in open areas and beneath shrub canopies. Air temperatures at 1.6 m were recorded concurrently with soil temperatures. We weighed soil samples, dried them for 72 h at 110°C, and then reweighed them to determine gravimetric soil moisture. Oven-dried soils were then used for soil pH, organic matter, and nutrient analyses. Soil organic matter and water potentials of *Coleogyne* shrubs were measured in May, July, and August 1994. Soil organic matter was determined from ash remaining after soils were heated to 550°C for 4 h. We measured soil compaction in open areas in August 1994 using a penetrometer that was inserted into the soil after we had removed stony surface pavements. Total Kjeldahl nitrogen (TKN), total Kjeldahl phosphorus (TKP), soil depth, and soil pH were measured in August 1993. Total nitrogen and phosphorus were determined on oven-dried soils following acid digestion using a modified Kjeldahl method (Page 1982) for rapid flow-through analysis of soil extracts. Soil depth was estimated by determining the depth to which a steel rod could be pounded into undisturbed soils. Soil pH was determined from a slurry consisting of equal parts of soil and distilled water. No edaphic measurements were made during winter months due to the presence of snow on the ground at the upper portions of the lower *Coleogyne* ecotone.

In June 1993, within each of the 27 plots that contained *Coleogyne*, we measured the following characteristics of *Coleogyne:* water potential, stem growth, and nutrient status (TKN, TKP) and biomass production of stems and leaves. We measured water potentials on 10- to 20-cm-long terminal branches of *Coleogyne* shrubs at predawn and midday in May and August 1994 using a portable pressure chamber and nitrogen gas. Twenty terminal twigs from 1 *Coleogyne* bush (approximately 45–60 cm canopy diameter) were harvested in June 1994 for analysis of growth. The growth of *Coleogyne* normally begins in March and ceases in June (West 1983). Twig elongation was measured from March to June 1993. Stems and leaves of *Coleogyne* were collected and then oven-dried for 72 h at 60°C before weighing and analyzing for total nitrogen and phosphorus following acid digestion (Page 1982). Biomass of current-year stems and leaves was determined after oven-drying for 72 h at 60°C.

Statistical Analyses

One-way analysis of variance (ANOVA), followed by a Tukey's multiple comparison test (Analytical Software 1994), was used to detect differences among elevations in the lower elevational limits of *Coleogyne* and to compare site means when a significant elevation effect was detected. Pearsons correlation analysis was performed to correlate biotic and abiotic factors with *Coleogyne* density. Soil moisture, soil organic matter, and soil and plant nutrient percentages were arcsine-transformed prior to statistical analysis. Multiple analysis of variance (MANOVA) was used to detect significant effects of elevation, depth, month, time, and year on soil moisture, soil organic matter, soil temperature, and water potential of *Coleogyne*. Mean values are expressed with standard errors, and significance was determined at $P \leq 0.05$.

RESULTS

The mean density of *Coleogyne* increased significantly ($P < 0.0001$) as elevation increased across the lower ecotone (Fig. 1). Soil temperatures (Figs. 2A, 2B) declined significantly with increasing elevation across the lower ecotone by month and depth ($P < 0.0001$) and were cooler under shrubs than in the open ($P < 0.05$). All possible interactions (open space–shrub canopy, soil depth, month, and elevation) were also significant ($P < 0.01$). Temperatures were usually cooler at higher elevations and under shrub canopies.

Coleogyne density was negatively correlated with air temperatures ($r = -0.95$, $P < 0.001$) across the lower boundary in Lucky Strike Canyon. Air temperatures were also significantly different ($P < 0.0001$) among the 3 summer months (data not shown).

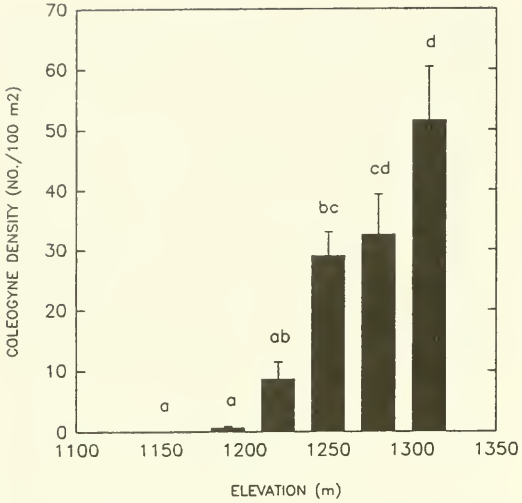

Fig. 1. Density of *Coleogyne* along its lower ecotone ($n = 6$; mean ± $s_{\bar{x}}$). Narrow vertical bars denote standard errors of the means. Columns labeled with different letters are significantly different at $P < 0.05$.

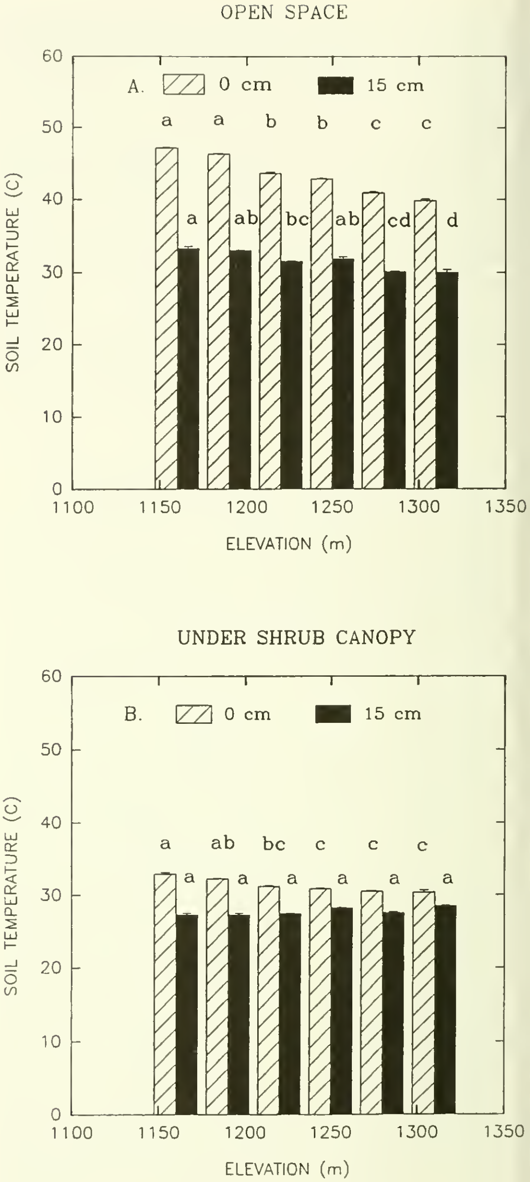

Fig. 2. Soil temperatures at the soil surface and at depths of 15 cm in open spaces (A) and under shrub canopies (B) in August 1993 ($n = 36$ in each treatment; mean ± $s_{\bar{x}}$). Narrow vertical bars denote standard errors of the means. Columns labeled with different letters are significantly different at $P < 0.05$.

Soil moisture (Table 2; 0–7 cm soil depth) increased with elevation ($P < 0.0001$) but also varied by month (May, July, and August; $P < 0.0001$) and year (1993, 1994; $P < 0.0001$). Significant interactions for soil moisture were detected between soil depth (0–7 and 7–15 cm) and year ($P < 0.05$), soil depth and month ($P < 0.0001$), and between soil depth, month, and elevation ($P < 0.05$).

A similar pattern of soil moisture was seen at depths of 7–15 cm as well as among the summer months and between the 1993 and 1994 years. Soil moisture percentage was the highest in the month of August 1993 (data not shown) because of summer storms that occurred from late July through mid-August.

Coleogyne shrubs were significantly more water stressed (more negative water potential values; Fig. 3) in August of 1994 at lower elevations at both predawn ($P < 0.001$) and midday ($P < 0.0001$). Water potentials were positively correlated with *Coleogyne* density at predawn and midday ($r = 0.95$, $P = 0.001$; $r = 0.97$, $P < 0.001$, respectively). Significant interactions were detected between water potential and month (May and August 1994; $P < 0.0001$). *Coleogyne* shrubs experienced more water stress in May than in August, although a similar pattern was detected between these months. Bowns (1973) proposed that shedding of leaves is an adaptive feature for conserving water, which is the factor limiting growth and development of *Coleogyne*. All possible interactions (month, elevation, and time) were also significant ($P < 0.05$).

Coleogyne density was positively correlated with soil organic matter ($r = 0.93$, $P < 0.001$). Soil organic matter at 0–7 cm depth was significantly greater as elevation increased (Table

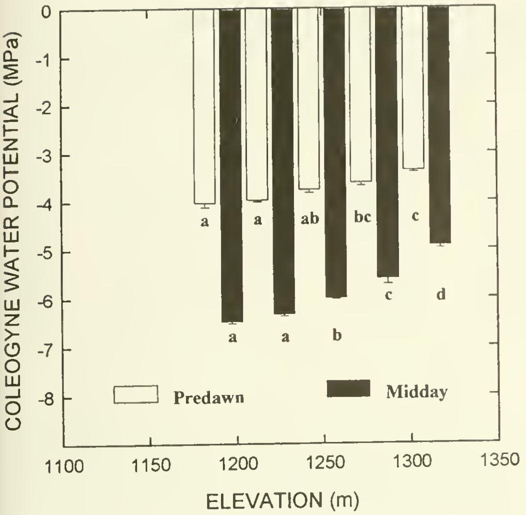

Fig. 3. Predawn and midday water potentials of *Coleogyne* shrubs across the lower ecotone in August 1994 (n = 15 in each treatment; mean ± $s_{\bar{x}}$). Narrow vertical bars denote standard errors of the means. Columns labeled with different letters are significantly different at $P < 0.05$.

TABLE 1. Pearsons correlation coefficients of *Coleogyne ramosissima* density to various biotic and abiotic factors of *Coleogyne*. All factors were measured during 1993 except soil compaction (August 1994). Nitrogen and phosphorus values were determined by Kjeldahl digestion.

Factor	r
Soil organic matter	
0–7 cm	0.93^{***}
7–15 cm	0.89^{***}
Soil compaction	-0.89^{***}
Soil nitrogen	
0–7 cm	0.37^{*}
7–15 cm	0.39^{*}
Coleogyne nitrogen	
stems	-0.86^{***}
leaves	-0.87^{***}
Soil phosphorus	
0–7 cm	0.26^{NS}
7–15 cm	0.68^{***}
Coleogyne phosphorus	
stems	0.99^{***}
leaves	0.80^{***}
Coleogyne biomass	
stem	-0.92^{***}
leaves	0.50^{**}
Coleogyne stem elongation	-0.52^{**}
Soil depth	-0.48^{**}
Soil pH	
0–7 cm	-0.42^{NS}
7–15 cm	-0.62^{NS}

$^{*}P < 0.05$
$^{**}P < 0.01$
$^{***}P < 0.001$
NS = nonsignificant

2; $P < 0.0001$). A similar pattern was seen at depths of 7–15 cm (data not shown). There was also a significant interaction ($P < 0.05$) between elevation and soil depth.

Coleogyne density was negatively correlated with soil compaction (Table 1). Greatest soil compaction occurred at *Larrea-Ambrosia* stands at lower elevations, and least compaction occurred in nearly monospecific *Coleogyne* stands at higher elevations (Table 2; $P < 0.0001$).

Total soil Kjeldahl nitrogen (TKN) at 2 depths did not exhibit a consistent pattern with elevation ($P > 0.05$), and *Coleogyne* density was weakly positively correlated with total soil nitrogen at 0–7 cm or 7–15 cm (Table 1). The upper 7 cm generally had higher TKN than the soils 7–15 cm deep. Total soil phosphorus (TKP) in the upper 7 cm of the soil did not vary with elevation ($P > 0.05$), and *Coleogyne* density was not significantly correlated with total soil phosphorus (Table 1). The highest TKP values occurred at an elevation of 1280 m, which was just below the nearly pure *Coleogyne* stands; the lowest TKP values were in *Larrea-Ambrosia* stands (1160 m).

Total nitrogen content in *Coleogyne* stems declined significantly (Table 3; $P < 0.05$) as elevation increased, and *Coleogyne* density was negatively correlated with total *Coleogyne* stem nitrogen (Table 1). *Coleogyne* leaf nitrogen content, consistently higher than stem nitrogen, did not differ significantly along the lower elevational limit of *Coleogyne* (Table 3; $P > 0.05$).

Total phosphorus content in *Coleogyne* stems did not increase significantly (Table 3; $P > 0.05$) with elevation along the lower ecotone, but *Coleogyne* leaf phosphorus content did increase significantly (Table 3; $P < 0.05$) with elevation.

Mean soil depth did not differ significantly with increasing elevation ($P > 0.05$) but was weakly negatively correlated with the density of *Coleogyne* (Table 1), although it declined slightly with elevation. The deepest soil was found at an elevation of 1190 m, the lowest elevation at which *Coleogyne* occurred.

Coleogyne density showed a weak negative correlation with soil pH at depths of 0–7 cm (Table 1) and did not vary with increasing elevation ($P > 0.05$). Soils near the center of the ecotone (1210 m) tended to have higher pH values than soils at other elevations.

TABLE 2. Soil moisture and soil organic matter at depths of 0–7 cm, soil compaction (kg/cm^2), and soil nutrients (TKN and TKP at 0–7 and 7–15 cm depths) along the lower *Coleogyne* ecotone. Mean values of soil moisture, organic matter, and nutrients are expressed in percentages and were arcsine-transformed. Columns labeled with different letters are significantly different at $P < 0.05$.

Elevation (m)	Soil moisture (%)	Soil OM (%)	Soil compaction (kg/cm^2)	Soil TKN		Soil TKP	
				0–7	7–15	0–7	7–15
1160	0.96a	—	7.6a	0.07a	0.04a	0.82a	0.63a
1190	1.03ab	2.9a	6.5ab	0.08a	0.03a	0.71a	0.65ab
1220	1.43abc	4.3ab	6.9ab	0.06a	0.03a	0.67a	0.73ab
1250	1.70bc	4.5ab	5.8bc	0.06a	0.02a	0.74a	0.72ab
1280	1.79bc	5.7ab	6.4ab	0.10a	0.06a	0.69a	1.00b
1310	2.00c	6.8b	5.0c	0.09a	0.05a	0.81a	0.82ab

Mean stem biomass of *Coleogyne* tended (nonsignificantly; $P = 0.0552$) to decrease with elevation (Table 3) and to be negatively correlated (Table 1) with *Coleogyne* density. Mean leaf biomass of *Coleogyne* (Table 3) showed no statistical significance across the elevational boundary, but *Coleogyne* density showed a weak positive correlation with *Coleogyne* leaf biomass (Table 1). Unlike stem biomass, leaf biomass tended to increase as elevation increased up to 1300 m.

Mean stem elongation of *Coleogyne* (3.87 ± 0.43 cm; Table 3) from March to June did not display a definite pattern across the lower ecotone of *Coleogyne* (Table 1; $P > 0.05$). The lowest mean stem elongation took place near the center of the ecotone, whereas the highest rate occurred in *Larrea-Ambrosia* stands. *Coleogyne* density was not significantly correlated with stem elongation (Table 1).

DISCUSSION

Abiotic factors appeared to limit the distribution of *Coleogyne* at its lower elevational boundary in Lucky Strike Canyon in southern Nevada. Previous studies have shown that low soil water content influences the distribution of *Coleogyne* at its lower ecotone in Utah (Bowns 1973). The appearance and persistence of *Coleogyne* at its lower elevational limit in Searchlight in southern Nevada is probably related to an increase in precipitation (Hunter and McAuliffe 1994). Precipitation is the major control of soil water content. However, no one has tested which edaphic factor may be most important in determining the distribution and density of *Coleogyne* in southern Nevada.

Soil temperatures were negatively correlated with *Coleogyne* density. Soil moisture reaches a minimum while soil temperature reaches a maximum in early summer in southwestern Utah (Bowns 1973). This pattern was more prominent in *Larrea-Ambrosia* stands (1160 m in elevation) where *Coleogyne* shrubs were absent and apparently could not tolerate a combination of relatively high soil temperatures and low soil moisture. Soil temperatures in open areas displayed a greater fluctuation and were consistently and significantly warmer than soil temperatures under shrub canopies. Shreve (1924) suggested that insolation is of more importance than air temperature in determining soil temperature. Little variation was observed between temperatures at 15-cm depth across the ecotone beneath canopies and in open spaces. Much of the fluctuation that occurs during late spring and summer can be attributed to changes in soil moisture content (Bowns 1973). Bowns and West (1976) reported that soil temperatures in *Coleogyne* communities start to increase in February and March, peak in June or July, but decline in August due to wet soils. Soil temperatures in our study did not decline in August despite moderately wet soils during the thunderstorm season. Soil moisture and temperatures at the Nevada Test Site in Mercury in southern Nevada do not always correspond to the lower temperature and increased precipitation associated with increases in elevation, but they are influenced by physiography and soil properties (Rickard and Murdock 1963).

Air temperatures in winter may influence the distribution of *Larrea-Ambrosia* at their upper elevational boundary. Beatley (1974) stated that the average extreme minimum air temperatures on all *Larrea-Ambrosia* sites are above −17°C. Variation in air temperatures along the lower boundary of *Coleogyne* in this study was 1°C because the plots covered only 150 m in elevation. Nevertheless, *Coleogyne*

Table 3. *Coleogyne* stem elongation (cm; $n = 20$ per bush), total *Coleogyne* stem and leaf nitrogen (TKN) and phosphorus (TKP), and *Coleogyne* biomass (g) along the lower *Coleogyne* ecotone ($n = 27$). Mean values of nutrient status are expressed in percentages and were arcsine-transformed. Columns labeled with different letters are significantly different at $P < 0.05$.

Elevation (m)	Stem elongation (cm)	Stem (%)		Leaves (%)		Biomass (g)	
		TKN	TKP	TKN	TKP	Stems	Leaves
1190	4.23a	0.58ab	0.43a	0.86a	0.92a	0.18a	0.03a
1220	4.05a	0.60a	0.46a	0.87a	1.21a	0.18a	0.04a
1250	3.57a	0.50ab	0.56a	0.76a	0.93a	0.14a	0.04a
1280	3.85a	0.40b	0.55a	0.81a	1.35ab	0.15a	0.05a
1310	3.83a	0.41b	0.62a	0.75a	2.17b	0.13a	0.03a

densities were negatively correlated with air temperatures.

Rickard and Murdock (1963) stated that soils of *Coleogyne* communities of Yucca and Frenchman flats in south central Nevada have more available moisture than *Larrea-Ambrosia* soils and that available moisture is greater in the subsurface (10–30 cm) than in the surface (0–10 cm). The lower limits of *Coleogyne* distribution may be a result of low soil moisture (Bowns and West 1976). Soil moisture in our study was positively correlated with *Coleogyne* density. *Coleogyne* growth ceased in mid-June, presumably due to limited soil water content. Soil moisture is greatest prior to the beginning of *Coleogyne* growth in mid-March. Exhaustion of soil moisture coincides with cessation of growth of *Coleogyne* in mid-June (West 1983). In fact, *Coleogyne* underwent summer dormancy, with no growth, around mid-June. No water potential readings of *Coleogyne* shrubs were recorded in July 1994. Bowns and West (1976) concluded that summer dormancy of *Coleogyne* is a result of soil moisture depletion rather than high air temperatures, and no chilling treatment is required to break dormancy. Plants exhibiting drought-induced summer dormancy have evolved to take advantage of water when it is present and to become dormant when water is scarce (Bowns 1973).

Soil organic matter increased with elevation across the lower *Coleogyne* boundary. Deposition of older and outermost *Coleogyne* leaves at the onset of summer dormancy and decomposition of winter ephemerals can generate a considerable amount of organic matter for the soil in *Coleogyne* communities (Bowns 1973). West (1983) stated that composition and productivity of annuals vary from year to year because they rely heavily on precipitation. *Bromus rubens* (red brome grass), a dominant winter ephemeral of many *Larrea-Coleogyne* ecotones between elevations of 1220 and 1310 m (Beatley 1966), tends to form carpetlike vegetation among shrubs in the spring season of wet years. It was not abundant in *Larrea-Ambrosia* stands. The presence of cryptogamic crusts can also increase organic matter in soils (Loope and Gifford 1972). *Coleogyne* zones in Lucky Strike Canyon exhibited a higher organic content than *Larrea-Ambrosia* communities presumably because of abundant *Bromus* ephemerals.

Coleogyne density was generally negatively correlated with soil compaction. Variations of soil compaction may play a secondary role in limiting the distribution of *Coleogyne* at its lower elevational boundary. Soils at higher elevations tend to have lower compaction primarily due to better infiltration; also, they are more permeable to air and water required by plant roots (Bowns 1973).

Algae, mosses, and lichens that form cryptogamic crusts appear to fix nitrogen in *Coleogyne* communities (Loope and Gifford 1972) and may increase fertility of the associated soils (Callison and Brotherson 1985). Total soil nitrogen did not exhibit a definite pattern across the lower *Coleogyne* ecotone. Total phosphorus remained fairly constant. *Coleogyne* leaves had a higher content of nitrogen and phosphorus than stems, which corresponds with Bowns (1973). *Coleogyne* leaves consistently stored more nutrients than stems. *Coleogyne* stems and leaves were relatively low in phosphorus. Nevertheless, Provenza (1978) proposed that phosphorus content is highest during the growing period but appears to decrease as the *Coleogyne* growth period continues through June.

Coleogyne stem biomass (g) per branch declined as *Coleogyne* became denser with elevation. On the other hand, *Coleogyne* leaf biomass (g) per branch increased slightly as the species became denser with elevation. This phenomenon may indicate a production of more current-season leaves as stem biomass declines with elevation.

The total rate of current-season stem elongation of *Coleogyne* did not vary significantly during the growing season throughout the lower elevational boundary. Nevertheless, relatively high air and soil temperatures may determine the rate of stem elongation in *Coleogyne*; periods of warm weather result in abundant growth, while cool periods retard the growth rate (Bowns 1973).

Coleogyne density was weakly negatively correlated with soil depth across the lower boundary at Lucky Strike Canyon. Soil depth declined slightly from the first appearance of *Coleogyne* to the nearly pure *Coleogyne* stands. However, Callison and Brotherson (1985) suggest that shallowness of soils is an important feature of *Coleogyne* communities and may partially determine the abundance and distribution of *Coleogyne*. Rooting patterns of *Coleogyne* enable the plant to extract water more efficiently from shallow and sandy soils than from deep soils (Korthuis 1988). The majority of *Coleogyne* roots are found at depths of 10–30 cm, and caliche layers are considered a major obstacle to many roots in southwestern Utah (Bowns 1973). Hence, roots of many shrubs run horizontally and contribute to a general decrease in root biomass moving from plants toward open areas between plants (Bowns 1973). Soil depth is a significant factor associated with *Coleogyne* density and distribution only when considering the entire mountain range, but not across its lower ecotone in southern Nevada (Lei 1995).

Soil pH did not differ significantly between *Larrea-Ambrosia* stands and the lower *Coleogyne* ecotone. Soil pH in *Coleogyne* communities in Utah ranges from 7.8 to 8.5, with no definite trends within the profile and sites (Korthuis 1988). Soil pH of lower *Coleogyne* limits ranged only from 7.8 to 8.0. High pH values are related to elevated levels of calcium and sodium in soils (Callison and Brotherson 1985). Hence, soil pH did not play a vital role in limiting *Coleogyne* distribution at Lucky Strike Canyon.

The scarcity of *Coleogyne* seedlings at its lower elevational boundary of Lucky Strike Canyon is indicative of infrequent reproduction (Lei personal observation 1994). However, we observed greater seedling densities at higher elevations. Seedling survival can be relatively high at high-elevational sites of the Colorado Plateau in southern Utah (Pendleton et al. 1995). Seeds are generated only in wet years when rains arrive during the winter or during spring growth (Bowns 1973). Survival of seedlings is exceedingly poor: young seedlings usually die as a result of inadequate soil moisture, and older seedlings are eaten and uprooted by rodents and rabbits (Bowns and West 1976). On the contrary, seedling survival can be relatively high at high-elevational sites of the Colorado Plateau in southwestern Utah.

Coleogyne density and distribution appear to be influenced by edaphic factors, particularly soil moisture and soil organic matter. *Coleogyne* also exhibits variations in stem elongation, as well as nutrient content (N and P) and biomass production of stems and leaves across its lower elevational boundary. Lucky Strike Canyon is representative of the vegetation and landscape conditions prevailing in southern Nevada. Experiments and establishment of long-term plots at various sites are necessary to further understand the complex relationships between the distribution of *Coleogyne* and associated biotic and abiotic factors in southern Nevada.

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VARIATION IN GERMINATION RESPONSE TO TEMPERATURE AND WATER AVAILABILITY IN BLACKBRUSH (*COLEOGYNE RAMOSISSIMA*) AND ITS ECOLOGICAL SIGNIFICANCE

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ABSTRACT.—Blackbrush (*Coleogyne ramosissima* Torr.) is a dominant desert shrub in a distinct mid-elevational vegetation belt between creosote bush–bursage (*Larrea tridentata–Ambrosia dumosa*) shrubland below and big sagebrush–pinyon pine–Utah juniper (*Artemisia tridentata–Pinus monophylla–Juniperus osteosperma*) woodland above in the Mojave Desert. Seed germination patterns of blackbrush seeds collected from 2 elevations (1200 and 1550 m) in 5 mountain ranges within the blackbrush shrublands were investigated. Morphological features of blackbrush seeds, including weight, length, and width, were not significantly different ($P > 0.05$) among elevations and mountain ranges in the Mojave Desert. Germination of blackbrush seeds was optimal when preceded by a prechill period of 4–6 wk. Seeds incubated at room temperature germinated poorly. Seeds collected at warm, low-elevation sites appeared to be less dormant (required less prechill time), germinated faster, and showed a higher overall germination response at low temperature relative to cold, high-elevation sites. Frequencies of watering also determined the germination response; watering at 2-wk intervals revealed the greatest germination. Some ecotypic variation among populations establishing at different elevations was evident with regard to dormancy duration and germination response at certain constant temperatures.

Key words: blackbrush, germination, elevation, prechill, temperature, watering frequency, ecotype, Mojave Desert.

Control and timing of the germination process are the keys in survival of plant populations whose principal mode of reproduction is from seed (Harper 1977, Meyer et al. 1989). The selection pressure operating at this phase of the life cycle must be strong, since only a tiny fraction of seeds survive to maturity (Meyer et al. 1989). Investigations between population differences in germination strategy within blackbrush (*Coleogyne ramosissima*) are infrequent. By holding aspects of life history and genetics background more or less constant, germination strategy variation of blackbrush in relation to temperature and moisture availability may be more evident.

Blackbrush was selected as a representative species for such a study because little attention has been focused on its germination biology. Previous studies have been limited to relatively small geographical areas in southern Utah and Nevada. A significant relationship exists between collection site elevation and seed germination response at 5–15°C, with and without a short 2-wk chill (Pendleton and Meyer 1994, Pendleton et al. 1995). Germination of blackbrush seeds requires a cold stratification (moist-chilling) at 4°C without light (Bowns 1973, Bowns and West 1976). This phenomenon could be advantageous because seeds can germinate from relatively deep in soils that rodents leave behind in the cache (Bowns and West 1976). Seeds collected from low-elevation sites are less dormant than seeds from high-elevation sites in southern Utah and Nevada (Pendleton et al. 1995). The correlation between dormancy status and elevation of collection site may indicate that blackbrush has evolved ecotypes at the germination level (Pendleton et al. 1995).

The aim of this study was to discover the existence of possible geographical and elevational ecotypes within blackbrush populations that represent specific physiological adaptations to microenvironments in the various mountain ranges across the Mojave Desert. Seeds of 8 isolated populations of blackbrush from 5 major mountain ranges with different elevations were collected to examine variation in germination response to different temperature conditions and watering frequencies. Seed morphology among the 8 populations was also measured.

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METHODS

Seed Collection Sites

Blackbrush seeds from 8 populations were collected by Dr. Burton Pendleton and his colleagues in the Mojave Desert (Table 1) to determine germination strategies and requirements. Seeds of 4 populations were collected within the Spring Mountains (Table 1). Blackbrush often forms a well-defined, mid-elevational band between creosote bush–bursage below and big sagebrush–pinyon pine–Utah juniper woodland above. Elevations of blackbrush shrublands ranged from 1000 to 1850 m above sea level. The vegetation of this community was dominated by a closely spaced matrix of low blackbrush with a scattered distribution of other woody taxa (Bowns 1973).

Seeds were obtained from Dr. Pendleton and his colleagues of the Shrub Sciences Laboratory in Provo, Utah. They collected at 2 elevations (1200 and 1550 m) on 5 mountain ranges in late June through July 1994 to represent an elevational gradient covering a relatively small geographical area. Major mountain ranges and collection sites were selected on the basis of full establishment of blackbrush shrublands and seed availability, respectively. Flowering of blackbrush generally occurred in May and relied heavily on winter and spring precipitation. Anthesis, occurring over a period of 1–2 wk, was not synchronous throughout the elevations of blackbrush shrublands (Pendleton 1994). Seeds at higher elevations generally had a shorter flowering period and were freshly collected in late June, whereas seeds at lower elevations had a longer flowering period and were freshly collected in July 1994 (Pendleton personal communication 1994).

TABLE 1. Location of blackbrush seed collections on 8 major mountain ranges arranged alphabetically in southern Utah, Nevada, and northwestern Arizona. Approximate elevation of each collection site is shown. Four blackbrush populations were sampled within the Spring Mountains. Collections were made at the full establishment of blackbrush shrublands and were utilized in the temperature and moisture experiments.

Location	Elevation of collection site (m)
McCullough Range, NV	1200
Mormon Range, UT	1550
Sheep Range, NV	1550
Spring Mountains, NV	
Kyle Canyon	1550
Lee Canyon	1550
Mt. Potosi	1200
Red Rock Canyon	1200
Virgin Mountains, AZ	1200

Germination Experiments

Approximately 9600 blackbrush seeds were initially utilized in 3 different temperatures and 3 different watering frequencies with all possible combinations of these 2 treatments under laboratory conditions. Some seeds were incubated at 4°C, 14°C, and room temperature (24°C) without dry prechill, while others were preceded by dry-chilling treatments at 2°C for 2, 4, and 6 wk prior to initiating germination experiments in a laboratory at the UNLV campus. During experimental treatments blackbrush seeds were covered by 2 layers of moist filter papers in closed petri dishes. Approximately 25 seeds were placed on each culture, with 30 replicates in each of the 6 major experimental conditions. Seeds were incubated at room temperature (24°C), as well as in a cool chamber (4°C and 14°C) for 8 wk without light, but were briefly exposed to soft-white fluorescent light as germinated seeds were counted and recorded. Seeds from 8 populations were subjected to 3 different water frequencies (every 3 and 2 wk, and once a week with an amount of 5 ml), and to 4 dry prechill periods (no chill, prechill at 2, 4, and 6 wk). The germination of each population was observed within 2 wk of the initial experiments. Germination percentages were recorded at weekly intervals for 8 consecutive weeks, and mean germination values were arcsine-transformed. Emergence of radicles was the criterion for germination. Morphological features, such as seed weight and dimensions, were also used to discover variations among the 8 isolated blackbrush populations across the Mojave Desert.

Statistical Analysis

One-way analysis of variance (ANOVA), followed by a Tukey's multiple comparison test (Analytical Software 1994), was used to detect differences among seed morphological traits from 8 isolated populations, and to compare means of morphological traits from the 2 elevations and several geographical locations. Multiple analysis of variance (MANOVA) was employed to detect significant effects of elevation, temperature, and watering frequency on

TABLE 2. Mean weight, length, and width with standard errors of blackbrush seeds collected from 8 mountain ranges in southern Utah, Nevada, and northwestern Arizona ($N = 100$ per population in each measurement). Mountain ranges are arranged alphabetically, and 4 blackbrush populations were from the Spring Mountains. Mean values followed by the same letter within columns are not significantly different at $P < 0.05$. Mountain ranges followed by asterisks indicate high-elevation sites.

Population	Weight (mg)	Length (mm)		Width (mm)	
		Mean	$s_{\bar{x}}$	Mean	$s_{\bar{x}}$
McCullough Range	22	5.13a	0.17	3.68a	0.11
Mormon Range*	24	5.18a	0.12	3.83a	0.12
Sheep Range*	23	5.19a	0.17	3.79a	0.16
Spring Mountains, NV					
Kyle Canyon*	24	5.17a	0.19	3.82a	0.15
Lee Canyon*	23	5.14a	0.16	3.75a	0.13
Mt. Potosi	24	5.13a	0.16	3.69a	0.11
Red Rock Canyon	22	5.02a	0.15	3.65a	0.14
Virgin Mountains	23	5.15a	0.18	3.78a	0.15

seed germination rate. Mean values of seed dimensions were presented with standard errors, and significance was determined at $P < 0.05$.

RESULTS AND DISCUSSION

Seeds were collected from 8 isolated populations in southern Utah, Nevada, and extreme northwestern Arizona (Table 1). Morphological characteristics of blackbrush seeds were not significantly different ($P > 0.05$; Table 2) in terms of weight, length, and width among the 8 populations across the Mojave Desert (Table 2). Germination experiments under laboratory conditions showed various responses to 3 different temperature conditions and 3 watering frequencies. All possible interactions (elevation, temperature, and watering frequency) were significant ($P < 0.01$) on germination rate. Germination of blackbrush seeds was significantly greater ($P < 0.05$) incubating at 4°C (cold, moist stratification) than incubating at 14°C and 24°C without dry prechill and preceded by 3 chill periods (Table 3). Seeds from all populations responded well to cold stratification, especially when they were preceded by chill treatments of 4 and 6 wk. Cold stratification at 4°C without light is required for blackbrush seeds to break dormancy and germinate (Bowns 1973, Bowns and West 1976). Radicle protrusion was from the narrow, bent portion of a seed (Bowns 1973). A cold stratification requirement may function as an effective mechanism to prevent germination at a season when prevailing conditions are unfavorable for seedling survival (Capon et al. 1978). Seeds from all populations that were incubated at room temperature, on the contrary, began to experience fungal growth approximately 2 wk from the initial experiments with an exception of the 6-wk dry prechill period (Table 5). The fungi became significantly more evident throughout the cultures after 4 wk, and seed viability was severely damaged. No seeds survived beyond 6 wk after the initial experimental treatments (Table 5).

Cold stratified seeds experiencing no dry prechill yielded fairly low germination percentages from both elevations, although seeds from lower elevational sites tended to have higher percentages (Table 3). Collections made in different mountain ranges across the Mojave Desert from the same elevations behaved similarly in germination pattern and response (Tables 3–5). However, seeds collected from warmer, lower elevational sites (1200 m) had a higher germination response after a chill as short as 2 wk than those seeds collected from colder, higher elevational sites (1550 m) at a constant low temperature. My results support the suggestion by Meyer and Pendleton (1990) that germination patterns vary as a function of climate and elevation within a species. Seeds also responded to a long chill, but often yielded a lower germination percentage.

Seeds collected from colder, higher elevational sites responded poorly to short chill, but responded well to both intermediate (4 wk) and long (6 wk) chill periods at 3 constant temperatures (Tables 3–5). Long chill was required for complete removal of dormancy for seeds found at high elevations (Meyer and Pendleton 1990). Seeds may break dormancy in early spring after experiencing winter chill under

TABLE 3. Mean germination response of blackbrush seeds at 4°C without light and dry prechill, as well as preceded by 2, 4, and 6 wk of dry-chilling from 8 isolated populations. Seeds were subjected to 3 different watering frequencies (at 1-, 2-, or 3-wk intervals). All mean germination values are expressed in percentages and were arcsine-transformed (N = 1000 per population per treatment). Mountain ranges followed by asterisks indicate high-elevation sites. Row values followed by different letters are significantly different at $P < 0.05$.

	Watering frequency per treatment											
Population	No prechill			2-wk chill			4-wk chill			6-wk chill		
	1	2	3	1	2	3	1	2	3	1	2	3
McCullough	15e	29d	18e	29d	37c	34cd	90b	94ab	92b	97a	98a	97a
Mormon*	10e	12e	10e	20d	40c	39c	82b	91ab	86b	94a	96a	95a
Sheep*	14f	18e	12f	23d	34c	31c	85b	93ab	87b	96a	97a	94ab
Kyle Canyon*	8f	16e	10f	22d	34c	30cd	85b	92ab	89b	91ab	96a	97a
Lee Canyon*	10g	14f	13f	21e	32d	28de	81c	92ab	88b	90b	98a	93ab
Mt. Potosi	19f	25e	19f	39d	48c	34d	86b	89b	88b	95ab	99a	96ab
Red Rock	22f	27e	19g	35d	55c	34d	93b	97a	94ab	95ab	97a	98a
Virgin	19f	18f	11g	32e	47c	41d	91b	93ab	93ab	94a	95a	96a

TABLE 4. Mean germination response of blackbrush seeds at 14°C without light and dry prechill, as well as preceded by 2, 4, and 6 wk of dry-chilling from 8 isolated populations. Seeds were subjected to 3 different watering frequencies (at 1-, 2-, or 3-wk intervals). All mean germination values are expressed in percentages and were arcsine-transformed (N = 1000 per population per treatment). Mountain ranges followed by asterisks indicate high-elevation sites. Row values followed by different letters are significantly different at $P < 0.05$.

	Watering frequency per treatment											
Population	No prechill			2-wk chill			4-wk chill			6-wk chill		
	1	2	3	1	2	3	1	2	3	1	2	3
McCullough	1g	1g	0g	19ef	24e	17f	62d	72c	69c	91b	97a	94ab
Mormon*	1g	4g	0g	12f	22e	15f	60d	67c	64cd	86b	94a	91ab
Sheep Range*	0f	1f	0f	13e	16e	13e	56d	65c	59cd	87b	93a	90ab
Kyle Canyon*	2f	2f	1f	13e	21d	17de	64c	74b	70bc	88a	89a	90a
Lee Canyon*	1g	1g	1g	14f	21e	18ef	64d	70c	67cd	89ab	93a	88b
Mt. Potosi	3g	3g	3g	21f	26e	22ef	67d	76c	71cd	88ab	92a	91a
Red Rock	3f	3f	3f	18e	25d	22de	71c	83b	77c	84b	94a	93a
Virgin	3g	2g	2g	19f	27e	23ef	73d	79c	77cd	89b	95a	91a

TABLE 5. Mean germination response of blackbrush seeds at 24°C without light and dry prechill, as well as preceded by 2, 4, and 6 wk of dry-chilling from 8 isolated populations. Seeds were subjected to 3 different watering frequencies (at 1-, 2-, or 3-wk intervals). All mean germination values are expressed in percentages and were arcsine-transformed (N = 1000 per population per treatment). Mountain ranges followed by asterisks indicate high-elevation sites. Row values followed by different letters are significantly different at $P < 0.05$.

	Watering frequency per treatment											
Population	No prechill			2-wk chill			4-wk chill			6-wk chill		
	1	2	3	1	2	3	1	2	3	1	2	3
McCullough	0e	0e	0e	0e	0e	0e	12d	16d	21c	78b	84ab	89a
Mormon*	0e	0e	0e	1e	1e	0e	15d	23c	20c	85a	78b	81ab
Sheep*	0e	0e	0e	0e	0e	0f	13e	18d	22c	86a	81b	80b
Kyle Canyon*	0f	0f	0f	0f	0f	1f	16e	21d	17e	79b	75c	86a
Lee Canyon*	0f	1f	0f	0f	0f	0f	12e	18d	14e	70c	83a	76b
Mt. Potosi	0e	0e	0e	1e	0e	0e	14d	16cd	18c	84b	85b	90a
Red Rock	1e	1e	0e	2e	1e	0e	19d	24c	25c	84ab	89a	78b
Virgin	0e	0e	0e	1e	0e	0e	13d	22c	21c	78b	87a	85a

natural field conditions (Meyer and Pendleton 1990). Although the results between 4- and 6-wk periods of cold stratified seeds were not significant, a slight variation in germination response is discernible (Table 3). Seed collections from cold sites showed a general pattern of slower initial germination after a short duration of chill and often yielded lower overall germination percentages after 8 wk relative to seed collections from warm sites during the cold stratification experiments (Tables 3–5).

Blackbrush seeds usually germinated best when water was applied at 2-wk intervals regardless of elevational sites. Conversely, watering at 1- and 3-wk intervals regardless of temperature conditions generally showed a significant reduction ($P < 0.05$) in germination percentages. Watering at 3-wk intervals reduced the germination rate on the cultures. A certain amount of watering must occur before seeds will break dormancy, perhaps to remove chemical inhibitors (Walton 1969). If only small amounts of chemicals are leached away by insufficient moisture, the seed replenishes the lost chemicals, and the dormancy period continues (Walton 1969). This phenomenon may apply to seeds that are supplied with low quantities and frequencies of water. Despite the presence of fungi, the overall effect of fungi on germination was significantly reduced when seeds were incubated at a constant low temperature compared to a constant room temperature. Hence, not only was cold stratification essential for seed germination, but the frequency and amount of watering were also vital to promote a relatively high germination percentage.

Variation in germination response to 3 constant low temperatures among seed collections at 2 elevations was detected at $P < 0.05$. Seeds from all elevations responded positively to a 2-wk chill, but the response of seeds from low-elevation sites was roughly twice that of seeds collected at high-elevation sites (Pendleton et al. 1995), which generally corresponds with my data. The general germination pattern is similar to patterns for many other desert shrubs growing at high elevations in the Intermountain area (Meyer and Pendleton 1990). Variation in populations within species may be related to variation in climatic conditions at the seed collection sites (Meyer and Pendleton 1990). This phenomenon suggests a relatively strong selection pressure for adaptive germination-timing strategies in response to climate (Meyer and Pendleton 1990).

Results suggest some ecotypic variation among seed collections at different elevations in the Mojave Desert. The idea of blackbrush being a paleoendemic species, showing little genetic variability, and perhaps on the way to extinction (Bowns 1973) was not completely supported. Blackbrush populations are relictual because they were probably once more widespread, and their current distribution represents a restriction in their range with time (Bowns 1973). Nevertheless, blackbrush exhibited a variation in the germination rate at different elevations from a relatively small geographical area in southern Utah and Nevada (Pendleton et al. 1995). This differentiation in germination response was also discovered among the isolated populations in mountain ranges across the Mojave Desert according to my results. The upper and lower elevational ecotypes were detected in terms of dormancy duration and seed germination response at certain constant temperatures. Differences in germination rate would not result in a significant species difference or a difference in the stand.

Evidence of packrat middens during the Quaternary has revealed that the creosote bush–blackbrush ecotone has undergone frequent migrations, moving up and down in elevation in response to climatic shifts (Phillips and Van Devender 1974, Cole and Webb 1985, Spaulding 1990, Pendleton et al. 1995). The changing of gene pool to adapt to new ranges with regard to climatic shifts has led to repeated and successful migrations of blackbrush along elevational and/or environmental gradients during the Quaternary period (Pendleton et al. 1995). For these reasons, blackbrush may not be regarded as a paleoendemic species. However, my germination studies covered only a relatively small geographical range in the Mojave Desert. Experiments and long-term investigations with various life stages of blackbrush are necessary to further discover the ecotypic and/or genetic variability of blackbrush across the entire southwestern desert region.

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DIPLOSTOMIASIS IN NATIVE AND INTRODUCED FISHES FROM YELLOWSTONE LAKE, WYOMING

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ABSTRACT.—Totals of 101 native Yellowstone cutthroat (*Oncorhynchus clarki bouvieri*), 27 introduced lake trout (*Salvelinus namaycush*), and 40 introduced longnose sucker (*Catostomus catostomus*) from Yellowstone Lake, Wyoming, USA, were examined for eye flukes. Metacercariae of the trematode fluke *Diplostomum* were in vitreous humor and/or lens of 94% of Yellowstone cutthroat trout, 92% of lake trout, and 78% of longnose sucker. Longnose sucker had 7% prevalence of infection in both lens and vitreous humor of metacercariae, while Yellowstone cutthroat trout had 3% and lake trout 8%. *Diplostomum spathaceum* was in lens tissue of 5% of infected Yellowstone cutthroat trout and 93% of longnose sucker; *Diplostomum baeri* was in vitreous humor of 92% each of infected Yellowstone cutthroat trout and lake trout. Morphological characteristics indicate that a single species infected the lens of Yellowstone cutthroat trout and longnose sucker, while another species infected lake trout. Impacts of the parasite interchange between native and introduced fishes of Yellowstone Lake, Wyoming, are unknown but should be monitored each year.

Key words: Diplostomum, *metacercariae,* Oncorhynchus clarki, Salvelinus namaycush, *introduced fish, Wyoming.*

Eye fluke disease or diplostomiasis is a parasitic fish disease caused by strigeoid trematodes (Trematoda: Diplostomatidae), primarily of the genus *Diplostomum*. The parasite was first reported in the New Jersey State Hatchery at Hackettstown during 1937 and 1938, where it caused considerable damage to several fish species (Palmer 1939). Thousands of rainbow trout (*Oncorhynchus mykiss*) blinded by *Diplostomum spathaceum* were destroyed at the state fish hatchery in New Jersey (Ferguson and Hayford 1941). Metacercariae of strigeoid trematodes caused similar problems in Europe (Bauer et al. 1969, Schäperclaus 1991).

Brassard et al. (1982a) reported that the penetration of *D. spathaceum* cercariae into the host was directly proportional to exposure and involved chance contacts between host and parasite. There is a significant decrease in the proportion of penetrating cercariae that become established in the fish lens at a high exposure density, suggesting that many cercariae die before reaching this destination. *Diplostomum spathaceum* appears to reduce host survival rates. The host death rate increases exponentially rather than linearly with parasite burden under natural conditions (Anderson 1978).

Rau et al. (1979) and Pennycuick (1971) examined frequency distributions of *D. spathaceum* in natural fish populations and found a high parasite frequency within these populations. This may ensure that relatively few fish succumb to direct effects of the infection. The direct effect of *D. spathaceum* is only 1 component of rate of parasite-induced host mortality. Another component is the degree to which a parasite reduces the host's vigor and hence increases susceptibility to predation (Anderson 1978). It has been suggested that heavily parasitized fish are preferentially taken by predators (Pennycuick 1971, Crowden and Broom 1980). Brassard et al. (1982b) showed experimentally that even light infections with *D. spathaceum* cercariae predispose fish to predation.

Earlier studies of the parasites of cutthroat trout (*Oncorhynchus clarki bouvieri*) from Yellowstone Lake reported no infections by *D. spathaceum* (Heckmann 1971). Subsequently, Heckmann and Ching (1987) found metacercariae of *D. spathaceum* in longnose sucker (*Catostomus catostomus*) and *D. baeri* in Yellowstone cutthroat trout of Yellowstone Lake. Furthermore, Dwyer and Smith (1989) found *D. spathaceum* in the lens of longnose sucker and *Diplostomum* sp. in the vitreous humor and retina of Yellowstone cutthroat trout. Heckmann (1994) reported *D. spathaceum* and *D. baeri bacculentum* from Yellowstone cutthroat trout from Yellowstone Lake.

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Lake trout (*Salvelinus namaycush*), first caught in Yellowstone Lake during 1993 and 1994, has the potential to upset the ecological balance of Yellowstone Lake and the surrounding area (Kaeding et al. 1996). It is a major problem for the future of the lake's native cutthroat trout, the only native fish of the lake (Kaeding et al. 1996). Introduction of lake trout may have affected the densities of cutthroat trout, and it is probable that parasites were introduced along with the lake trout. Effects of any such parasite are unknown, as are effects of the native parasitofauna on the introduced lake trout. Dynamics of the parasitism may be important in the ultimate outcome of the invasion of lake trout into Yellowstone Lake. A recent example of the effect of parasites introduced with fish is that of the Asian fish tapeworm (*Bothriocephalus acheilognathi*) introduced to the Virgin River with infected fish from Lake Mead; these parasites had devastating effects on new fish hosts (Heckmann et al. 1986, 1987).

The purpose of our research is 2-fold. First, we discriminate the different *Diplostomum* spp. infecting fishes in Yellowstone Lake, and second, we evaluate possible interactions of parasites infecting native and introduced species.

MATERIALS AND METHODS

During 1994 and 1995 we gill-netted 168 specimens of 3 fish species in Yellowstone Lake, Yellowstone National Park, through the cooperation of park fisheries biologists. Fish heads were removed, fixed in buffered 10% formalin, and dissected in the laboratory. Metacercariae found in the lens and vitreous humor were

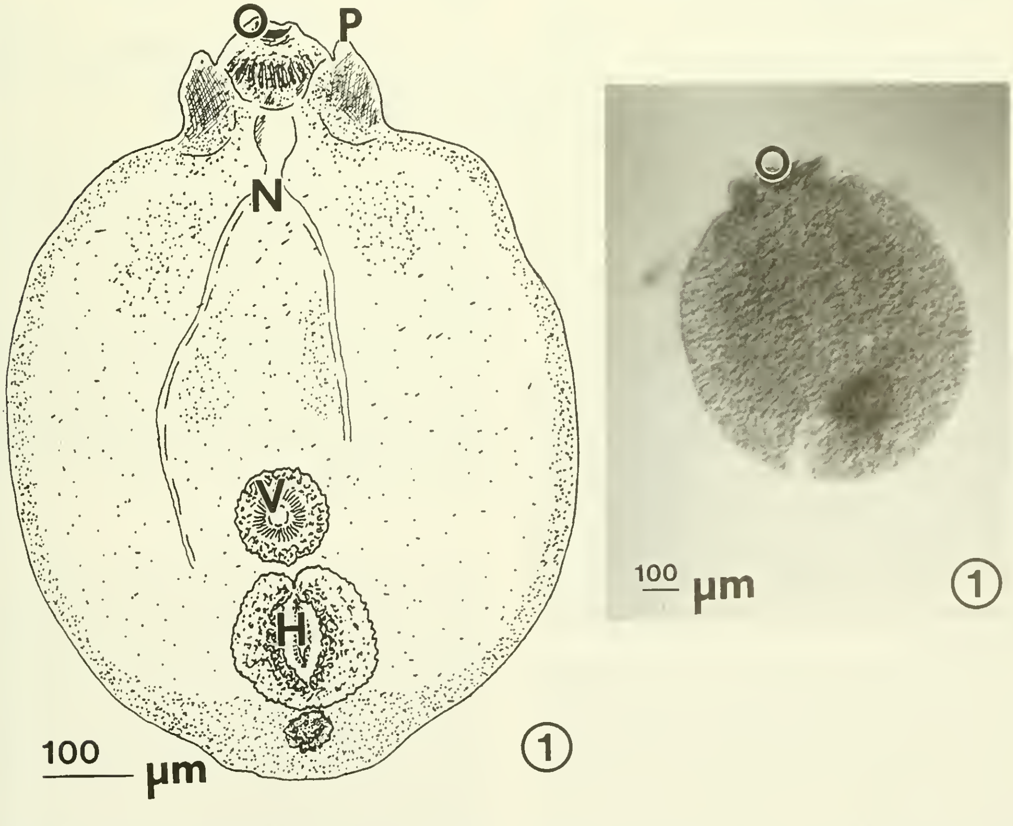

Fig. 1. Metacercariae of *Diplostomum spathaceum* found in the lens of *Oncorhynchus clarki bouvieri* (cutthroat trout) and *Catostomus catostomus* (longnose sucker); line drawing and light optics micrograph. H = holdfast organ, N = intestine, O = oral sucker, P = pseudosuckers, V = ventral sucker. Bar = 100µm. Magnification 100X for photo.

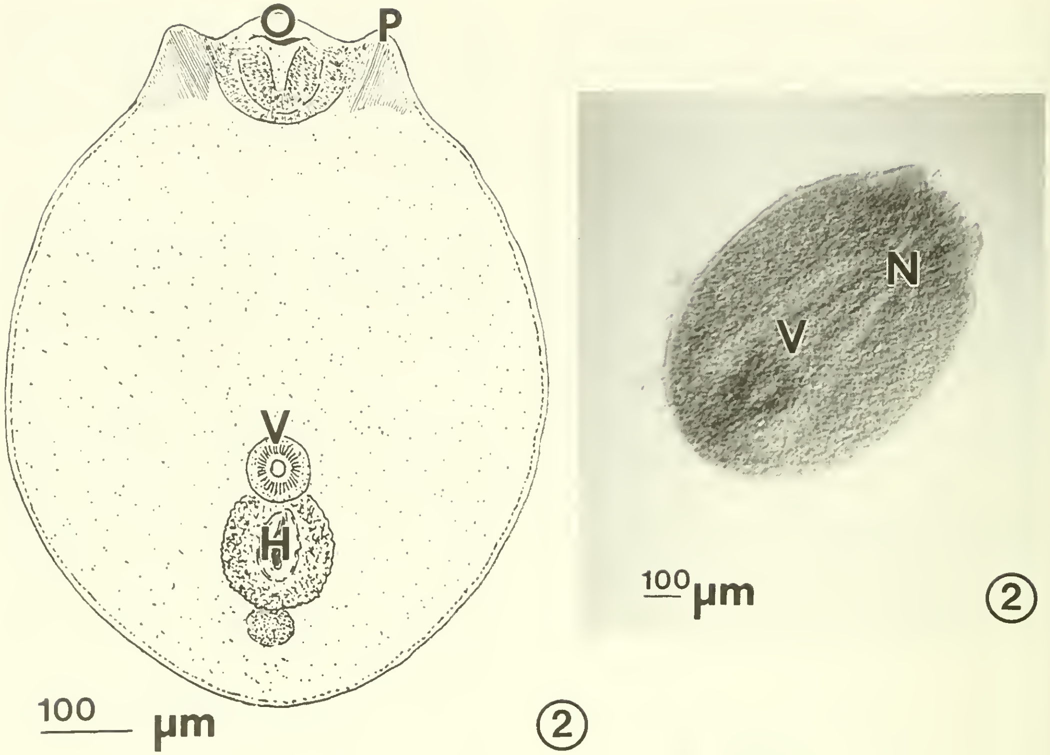

Fig. 2. Metacercariae of *Diplostomum baeri* found in the vitreous humor of *Oncorhynchus clarki bouvieri* (cutthroat trout); line drawing and light optics micrograph of the metacercariae. H = holdfast organ, N = intestine, O = oral, P = pseudosuckers, V = ventral sucker. Bar = 100µm. Magnification 100X for photo.

isolated, stained with Semichon's carmine, decolored with acid-alcohol, and whole-mounted in Permount (Sheehan and Hrapchak 1973, Lillie 1991). Drawings of metacercariae were made using camera lucida and an American Optical compound light microscope.

We recorded the following measurements from 20 metacercariae of each trematode species: body length and width, oral sucker length and width, pharynx length and width, ventral sucker length and width, holdfast organ length and width, distance from oral sucker to ventral sucker, and distance from oral sucker to holdfast organ. Data were then statistically analyzed using Number Cruncher Statistical Software.

Eyes of infected fish were fixed in buffered 10% formalin and processed by standard histological techniques (Sheehan and Hrapchak 1973, Lillie 1991). Paraffin-embedded tissue was sectioned at 4–6 µm and stained with hematoxylin and eosin, Mallory's trichrome, and toluidine blue. Slides were examined with a compound light microscope to help determine species of metacercariae present. Metacercariae were identified with available keys and descriptions (Hoffman 1967, Bauer 1985, Shigin 1986).

To further evaluate species of metacercariae, we processed samples for scanning electron microscopy (SEM) following standard techniques (Dawes 1994). Gold-coated samples were viewed with a JOEL 8400 Scanning Electron Microscope.

RESULTS

We collected longnose sucker, Yellowstone cutthroat trout, and lake trout at Yellowstone Lake. *Diplostomum* spp. metacercariae were found in the vitreous humor and/or lens of all 3 species. Prevalence of metacercariae was 78% in 40 longnose sucker, 94% in 101 Yellowstone cutthroat trout, and 93% in 27 lake trout. When both lens and vitreous humor were infected, we considered the result a mixed infection. Among infected fish, longnose sucker had 7% prevalence of mixed infections; 93% were

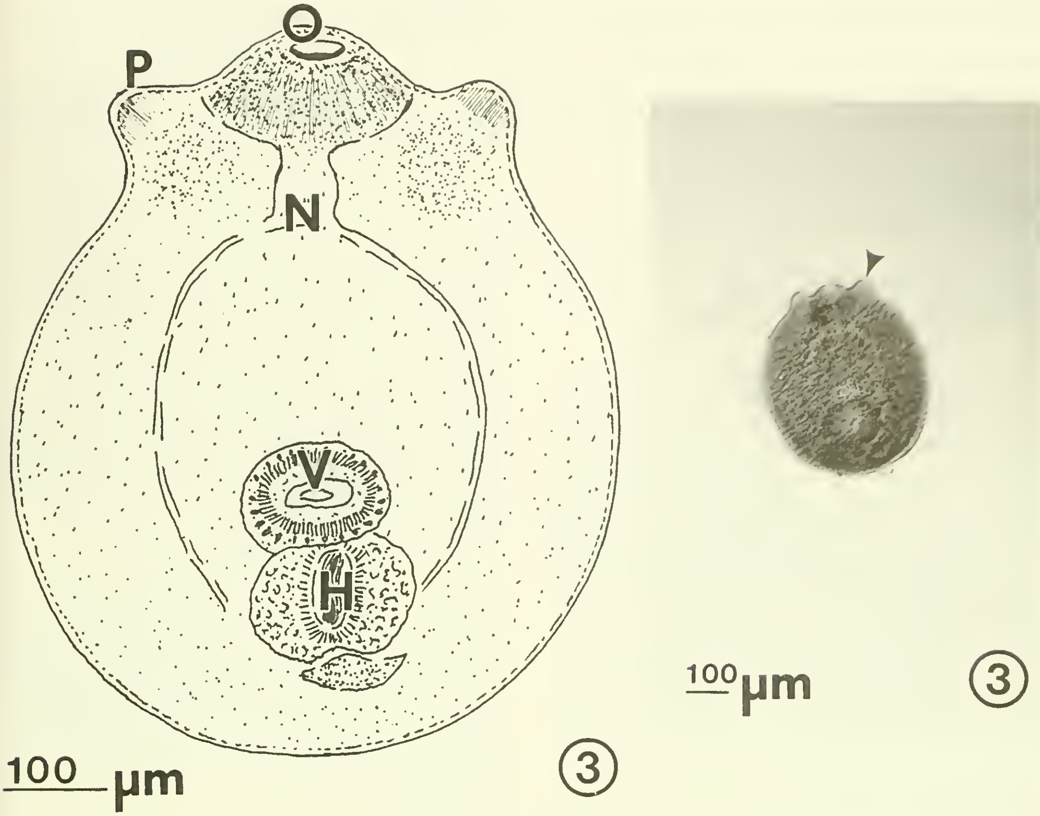

Fig. 3. Metacercariae of *Diplostomum* sp. from the vitreous humor of *Salvelinus namaycush* (lake trout), introduced into Yellowstone Lake; line drawing and light optics micrograph. Arrowhead = pseudosucker, H = holdfast organ, N = intestine, O = oral sucker, P = pseudosuckers, V = ventral sucker. Bar = 100µm. Magnification 100X for photo.

infected by *D. spathaceum* (Fig. 1) in the lens only. Three percent of Yellowstone cutthroat trout had mixed infections, 5% were infected in the lens by *D. spathaceum*, and 92% were infected by *D. baeri* (Fig. 2) in the vitreous humor. Eight percent of lake trout had mixed infections, and 92% were infected by *Diplostomum* spp. (Fig. 3) in the vitreous humor (Table 1).

Discriminant analysis of significant morphological measurements correctly classified 83% of the metacercariae according to occurrence in lens or vitreous humor. The same statistical analysis tabulated 93% accuracy in distinguishing among metacercariae infecting lens in longnose sucker and Yellowstone cutthroat trout. Discriminant analysis had 79% accuracy in distinguishing among metacercariae infecting vitreous humor in Yellowstone cutthroat trout and lake trout.

DISCUSSION

Besides upsetting an established ecological balance for the biota in Yellowstone Lake, Yellowstone National Park, the introduced lake trout may also introduce new parasites into the aquatic system. The change in parasitofauna may impact native fish in the lake. There is an established life cycle for diplostomiasis in the lake with fish containing metacercariae, a larval stage in the cycle.

Discriminant analysis using significant morphological measurements was 83.3% accurate in distinguishing between metacercariae infecting the 3 fish species localized in the lens or vitreous humor. Metacercariae from the different host species thus appear somewhat related. The same statistical analysis was 93% accurate in distinguishing metacercariae infecting the lens in longnose sucker and Yellowstone cutthroat

TABLE 1. Percent infection by metacercariae in fishes from Yellowstone Lake, Wyoming, 1994, 1995.

Host	Number (Infected)	Prevalence (%)	Metacercariae (%)		
			Mixed[a]	*D. spathaceum*	*Diplostomum* sp.
Longnose sucker *Catostomus catostomus*	40 (31)	78	7	93	0
Cutthroat trout *Oncorhynchus clarki*	101 (95)	94	3	5	92
Lake trout *Salvelinus namaycush*	27 (25)	93	8	0	92

[a] Includes *Diplostomum baeri*, both lens and vitreous humor infected.

trout, emphasizing the close taxonomic relationship these metacercariae have and the long-time coexistence of the 2 hosts in the lake. Thus, morphological characters differentiate the 2 different groups. For Yellowstone cutthroat trout and lake trout, discriminant analysis was 79.4% accurate in distinguishing metacercariae infecting the vitreous humor. These data are marginal for a close taxonomic relationship.

Statistical analysis using morphological characteristics of metacercariae substantiated similarity of those infecting lens of longnose sucker and Yellowstone cutthroat trout; thus they can be considered a single species (*D. spathaceum*). Morphological data also substantiated that metacercariae infecting Yellowstone cutthroat trout and lake trout can be considered different species. Preliminary DNA studies using standard techniques (Shiozawa et al. 1992) and arbitrary primers substantiated the morphological conclusions; additional DNA research is needed to strengthen this conclusion. Yellowstone cutthroat trout and longnose sucker are long-time residents in Yellowstone Lake; therefore, a nonspecific parasite such as *D. spathaceum* can infect both species. Lake trout, which has its own species of *Diplostomum* and other parasites, was caught and identified for the first time in Yellowstone Lake during 1993 and 1994. Impact of this newly introduced parasite is unknown and, depending on the definitive host (bird) and 1st intermediate host (mollusk), may impact native fish populations such as the Yellowstone cutthroat trout. Additional samples during future years will add important information to this assumption. The same possible impact may occur for the introduced species if the native *Diplostomum* and other parasites found in established Yellowstone Lake fishes become parasites of the lake trout population. Yearly surveillance of fish and parasites in Yellowstone Lake should be considered for proper ichthyofauna management. This will substantiate or refute damage of new hosts and parasites.

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WINTER SURVEY OF RAPTORS WITH NOTES ON AVIAN SCAVENGERS IN NORTHWESTERN COLORADO

Donald L. Beaver[1] and Jan J. Roth[2]

ABSTRACT.—Winter populations of raptors and scavengers were surveyed along 175 km of rural roads in Moffat County, northwestern Colorado. The survey began in 1988 and is currently continuing. Over the 7 yr of the survey reported here, we found Golden Eagles in high abundance ($\bar{x}$ = 5.8 km/eagle) compared to most studies in similar habitat. Bald Eagles were less abundant, but increasing compared to 20 yr earlier. American Rough-legged Hawks were in low abundance, probably due to the predominance of sagebrush habitat along the route. Northern Ravens were seen in low numbers in 4 yr. American Crows were seen in 2 yr. Black-billed Magpies were nearly as abundant ($\bar{x}$ = 6.5 km/magpie) as Golden Eagles and often scavenged with them. Magpie and Golden Eagle numbers were significantly correlated over the years of study. We conclude that northwestern Colorado is a significant overwintering area for Golden Eagles.

Key words: Golden Eagle, Bald Eagle, Black-billed Magpie, winter population, sagebrush, northwestern Colorado.

In the mid 1980s we noticed increased numbers of wintering Golden Eagle (*Aquila chrysaetos*) and Bald Eagle (*Haliaeetus leucocephalus*) in Moffat County, north and west of Craig, Colorado. In 1988 we initiated a long-term road survey to count raptors and other scavengers. The survey is currently ongoing. We report here the results of the first 7 yr of surveys.

STUDY AREA AND METHODS

The study area includes the northeast corner of Moffat County, which is located in the northwest corner of Colorado. Elevation ranges from 1860 to 2130 m, and the landform consists of rolling hills and gullies. Predominant vegetation is big sagebrush (*Artemisia tridentata*). The survey route is about 175 km in length, consisting of 3 adjoining segments that form an inverted triangle. The easternmost segment (55 km) follows the course of Fortification Creek to near its headwaters on Colorado Highway 13 north from Craig. The 2nd segment (45 km) follows the Little Snake River west on Moffat County Road 4. The westernmost segment (75 km) traverses the Great Divide area on Moffat County Road 7, ending just west of Craig. Utility poles and ledges are abundant along the route and serve as perch sites for raptors.

The survey was conducted from a van with 2 observers seated in the front and 1 or more in the back. Binoculars and a 20–30X spotting scope were used to identify and, in the case of Golden Eagles, age sighted birds. Golden Eagles were considered to be immatures if any white was seen in the wings or tail when flying. Birds could be seen on either side of the road a distance of about 0.5 km on the Colorado 13 and Moffat County 7 segments, and 1.0 km on the route along Moffat County 4, yielding an area of coverage approximately 220 km^2. We drove at a constant speed of 40–45 km/h over the route. Counts began between 0800 and 0900 MST and lasted 4–5 h. Surveys were conducted in the last week of December or the first 2 wk of January, which is midwinter in this area. The starting location of the route was alternated each year. All counts were made on calm days with no precipitation. The study began in the winter of 1988–89 and continued from 1990 through 1996.

RESULTS

Population Size

The Golden Eagle was the most abundant raptor in all years of the survey (Table 1). Their numbers peaked in 1991–92 and in 1993–94. The average distance traveled per Golden Eagle sighted was 5.8 km, with a range of 3.9–8.75 km/bird. Mean density was 0.23 eagles per km^2, or about 1 eagle per 4 km^2.

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TABLE 1. Total numbers of eagles, other large raptors, and scavengers seen on annual roadside surveys conducted at the end of December or early January in northwestern Colorado. Total length of the survey route was 175 km, and the area surveyed about 220 km^2.

	Survey year						
Species	1988–89	1990–91	1991–92	1992–93	1993–94	1994–95	1995–96
Golden Eagle	20	35	22	22	45	38	29
Bald Eagle	0	5	0	1	1	8	0
American Rough-legged Hawk	0	5	0	1	1	1	0
Prairie Falcon	0	0	0	0	1	0	0
Northern Raven	0	0	1	2	1	1	0
Black-billed Magpie	15	41	35	25	45	33	24
American Crow	7	0	1	0	0	0	0

We saw Bald Eagles in 4 of the 7 yr of the survey (Table 1). They occurred in low numbers and were seen primarily along the Little Snake River and upper reaches of Fortification Creek. The average sighting frequency was 53 km/Bald Eagle. Although Bald Eagle sightings have become more common in Moffat County during the last 10 yr compared with the previous 20 (personal observation), they are still found in low numbers.

Other wintering raptors and scavengers were less common than the Golden Eagle, with the exception of the Black-billed Magpie (*Pica pica;* Table 1), which was equally abundant ($\bar{x}$ = 5.9 km/bird). We counted few wintering hawks. Most numerous was the American Rough-legged Hawk (*Buteo lagopus*), which we saw on average every 153 km of route traveled. Other species, such as the Prairie Falcon (*Falco mexicanus*), Northern Raven (*Corvus corax*), and American Crow (*Corvus brachyrhynchos*), were infrequently sighted along the survey route and have not been observed during the last several years. These species are present and more numerous in other locations within the county (unpublished data).

DISCUSSION

Population Size

Population size of wintering Golden Eagles was higher than that reported by other workers in sagebrush habitat. Craig et. al. (1984) reported an average of 13.4 km and 12.5 km per Golden Eagle on a 187-km roadside survey in habitats similar to this study in southeastern Idaho in 1974–75 and 1975–76, respectively; the average in our study was 5.8 km/eagle. Woffinden and Murphy (1977), studying raptors along a 196-km survey route in habitats similar to ours in north central Utah, found Golden Eagles to be about 15-fold less numerous than we found (88 km versus 5.8 km per eagle in our study). In eastern New Mexico and western Texas, Boeker and Bolen (1972), studying wintering Golden Eagles by aerial techniques from 1963 through 1968, found much lower densities in Texas (average 0.006–0.008 eagles/km^2) but nearly equal densities in New Mexico to what we observed (average of 0.23 eagles/km^2). They did not describe the habitat of the regions they studied, so direct comparison is not possible. A roadside survey by Allan and Sime (1943) in the Panhandle of Texas yielded a very low number of wintering Golden Eagles (average of 865 km per eagle) over 4 yr of study (1938–1942). At least a portion of the habitat in the Panhandle was sagebrush. Enderson (1965), studying eagle populations in eastern Colorado during the fall and winters of 1962–63 and 1963–64, found lower numbers than we did (83.2 km per eagle) in short-grass prairie and agricultural fields. Ten years later Johnson and Enderson (1972) reported a 2.9-fold increase in abundance of wintering Golden Eagles along these same routes (29.8 km/bird).

Woffinden and Murphy (1977) found Bald Eagles to be more common than Golden Eagles, 22 km per eagle, compared to 53.3 km per eagle in our study. However, direct comparison with our study is probably unwarranted since their survey was for an entire year and included the breeding season. They did not report on winter numbers separately.

The low number of wintering hawks surprised us. Surveys along other routes in the county during the same years (unpublished data) showed Red-tailed Hawks (*Buteo jamaicensis*) and American Rough-legged Hawks were present in other localities. Craig et al. (1984) found many American Rough-legged Hawks in their study area. Woffinden and Murphy (1977) also found these hawks on their survey route in greater abundance than we did (73 km versus 153 km per hawk). Perhaps the preponderance of sagebrush habitat along our survey route did not favor *Buteo* presence. Consistent with our findings, Fischer et al. (1984), studying habitat selection of raptors in central Utah, found Red-tailed Hawks and Rough-legged Hawks to be more frequent in grassland, whereas Golden Eagles were more frequent in sagebrush.

Black-billed Magpies were often seen scavenging on road-killed animals along with Golden Eagles. The number of sightings of each species over the 7 yr fluctuated in concert ($P < 0.05$, Spearman $r = 0.77$; see Table 1), suggesting they shared the same food base. The high abundance of Black-billed Magpies along our survey route is consistent with Christmas count data for northwestern Colorado (Bock and Lepthien 1975). Direct comparison of our measure of abundance, km/bird, with Christmas count data is precluded because the data are in birds/party hour.

Age Distribution

Golden Eagles were aged in about 32% of the sightings early in the study, but this improved to 75% in the last 2 yr of the survey (see also Woffinden and Murphy 1977). Of the 67 birds assigned to an age category (adult or immature), 32% were immature. Our data suggest that relatively few immature birds winter in the area. We noted few interactions between adults and immature birds, and we often saw them perched near each other.

The extensive sagebrush habitat in northwestern Colorado provides a winter haven of some importance for Golden Eagles. Wintering concentrations are higher than reports from other regions in similar habitat. In combination with large expanses of similar habitat in southwestern Wyoming, the region probably provides a wintering site for a significant population of Golden Eagles. The region is not heavily impacted by human activities and is remote from most development. The greatest threat appears to be conversion of sagebrush to agricultural fields. Other raptors, and Northern Ravens and American Crows, are not as abundant in winter as reported elsewhere, possibly because of the preponderance of sagebrush, which is not favored by most raptor species (Fischer et al. 1984), and is not the main habitat of the large scavengers seen in this study.

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ERRATA

Correction to:

Ranne, Brigitte M., William L. Baker, Tom Andrews, and Michael G. Ryan. 1997. Natural variability of vegetation, soils, and physiography in the bristlecone pine forests of the Rocky Mountains. Great Basin Naturalist 57: 21–37.

Author Tom Andrews was incorrectly identified as an employee of the U.S. Forest Service. His correct address and affiliation are listed below:

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SPIDER WASPS OF COLORADO (HYMENOPTERA, POMPILIDAE): AN ANNOTATED CHECKLIST

Howard E. Evans[1]

ABSTRACT.—One hundred forty-three species of Pompilidae are recorded from Colorado, slightly more than half the number occurring north of Mexico. Some of these occur principally at higher altitudes or in the northern part of the state; this group includes 5 species of Holarctic distribution. Others (such as the tarantula hawks, *Pepsis*) are prevalent across the southern third of the state and range south into New Mexico and often into Mexico. Still others are widely distributed wherever there is friable soil suitable for nesting. Certain genera are more or less restricted to preying upon certain spider taxa, while others are generalists and a few are cleptoparasites of other Pompilidae.

Key words: Hymenoptera, Pompilidae, spider wasps, distribution.

Spider wasps are ubiquitous insects, occurring wherever there are spiders. They use these arthropods to provision their nests, employing a single paralyzed spider per cell. In Colorado they are most plentiful on the eastern plains, especially in sandy country along the valleys of the Arkansas and South Platte rivers. However, they also occur widely in the western two-thirds of the state, including the mountains. I have taken 61 species around my home, in open ponderosa pine–Douglas-fir woodland at 2300 m in Larimer County. The Holarctic species *Anoplius nigerrimus* (Scopoli) has been taken above timberline, at 3600 m on Trail Ridge, in Rocky Mountain National Park (Evans 1951). A female of *Anoplius tenebrosus* (Cresson), in good condition in the University of Colorado collection, is labeled as having been "caught in a snow drift" at 13,000 feet (3900 m) on Mt. Rogers, Clear Creek County. This individual was undoubtedly blown there by the wind.

Most Colorado species are believed to be univoltine, the adults active mid-June through early September. Only 1 species, *Anoplius tenebrosus* (Cresson), is known to overwinter as an adult; all others are believed to overwinter as diapausing larvae or pupae in their nest cells.

In this report I list 143 species from Colorado, slightly more than half the species known to occur north of Mexico. Only minimal data are included concerning habitat and behavior. Evans and Yoshimoto (1962) reviewed the nesting behavior of species occurring in the northeastern states, and many of these same species (and all genera) occur in Colorado. The most recent catalog of North American Hymenoptera (Krombein et al. 1979) includes further references. Major papers on the systematics of Nearctic Pompilidae are those of Evans (1950–51) and Townes (1957), although there have been several refinements in the classification in the decades since those papers were published.

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The Colorado fauna includes 5 species that also occur in Eurasia. These species range throughout the northern hemisphere and occur chiefly in the northern mountains: *Evagetes crassicornis* (Shuckard), *Anoplius nigerrimus* (Scopoli), *Arachnospila fumipennis* (Zetterstedt), *Caliadurgus fasciatellus* (Spinola), and *Ceropales maculata* (Fabricius). In contradistinction, quite a number of species characteristic of the deep Southwest and Mexico enter Colorado in the southernmost third of the state, for example, the species of *Pepsis* and *Psorthaspis*. Three species have been reported only from Montezuma County in extreme southwestern Colorado: *Calopompilus pyrrhomelas* (Walker), *Priocnemis oregona* Banks, and *Aporus luxus* (Banks).

Recently several species characteristic of eastern forests have appeared in Colorado, such as *Priocnemis minorata* Banks and *Auplopus mellipes variitarsatus* (Dalla Torre). Similarly, several typically West Coast species have been taken here, such as *Cryptocheilus hesperus* (Banks) and *Dipogon sericeus* Banks. It is possible that some of these species have been introduced in commerce.

Most spider wasps prepare simple nests in the soil, but a few make mud cells aboveground. A few oviposit on spiders directly, without taking them to a nest, and some are parasites of other Pompilidae (species of *Ceropales* and *Evagetes*). Most spider wasps are black in color, with translucent or fumose wings. A few have banded wings, and some (mostly larger species) have bright orange wings. Orange is an aposematic (warning) color in insects; it is believed that birds learn to associate this color with undesirable qualities (in this case a potent sting) and to avoid attacking such insects. Fifteen species occurring in Colorado have orange wings, forming a complex of what are often called Mullerian mimics. There are other examples of apparent mimicry: species with yellow banding, suggesting social wasps, and others with orange patterns on the body, suggesting Mutillidae (velvet ants).

The largest spider wasp in our fauna (and one of the largest in the world) is *Pepsis formosa* (Say), in which large females may have a body length of 5 cm and a wing span of 9 cm. In contrast, males of some of the smaller species of *Ageniella* have a body length of <2 mm, with a wing span of about 3 mm.

Adult spider wasps of most species take nectar at flowers, and it is here that most are taken by collectors. Flowers with shallow corollas, such as Apiaceae (Umbelliferae), are especially favored. Other genera that are frequently visited include *Asclepias, Baccharis, Cleome, Euphorbia, Melilotus, Sapindus, Solidago*, and *Tamarix*. Honeydew from extrafloral nectaries and from aphids and other sucking insects is also visited frequently, especially on *Helianthus*.

In this paper I accept the strictures of Menke (1990), though with misgivings, as these result in the use of several unfamiliar names for well-known species. Some of these novel synonymies are based on the discovery by Day (1977) of broken specimens with incorrect locality data that are claimed to represent North American species. Others are based on the rejection of secondary homonyms, an unfortunate procedure now evidently part of the code of zoological nomenclature.

I also accept the nomenclatural changes suggested by Shimizu (1994), based on his research and that of several European workers, most especially Day (1981). Arrangement of the genera follows that in the Catalog (Krombein et al. 1979) except in a few cases and with some changes in generic names. The list is based primarily on specimens in the collections of Colorado State University, Fort Collins; the University of Colorado, Boulder; and the Denver Museum of Natural History. Some records have been taken from the literature.

SUBFAMILY PEPSINAE

Genus *Calopompilus* Ashmead

This genus was called *Chirodamus* by Townes (1957), but the type of that genus is a South American species of doubtful affinities with North American species. These wasps are infrequently collected and nothing is known of their predatory or nesting behavior. Our 1 species has brilliant orange-red wings.

pyrrhomelas (Walker). Montezuma Co. A single female was collected 7 August 1929 by

P.R. Franke in Mesa Verde National Park. There is a female in the University of Wyoming collection from Laramie, WY, collected 26 September 1964 by R.E. Pfadt. The species was reported by Townes (1957) from British Columbia to Arizona, with no records from Colorado or Wyoming.

Genus *Pepsis* Fabricius

These are the "tarantula hawks," of large size and with bright orange wings. Females hunt for mygalomorph spiders ("tarantulas"), paralyze them by stinging, and place them either in the spider's burrow or in a shallow nest dug in the soil. Hurd (1952) reviewed the North American species and summarized data on behavior. Our 5 species are mostly confined to the southern third of the state.

angustimarginata Viereck. Otero and Pueblo counties.

formosa formosa (Say). Bent Co. Say described this species from the Arkansas Valley, and Hurd recorded it from several unspecified sites in southern Colorado, but it has rarely been collected there in recent years.

mildei Stal. Baca, Bent, Crowley, Otero, Prowers, and Pueblo counties.

pallidolimbata pallidolimbata Lucas. Mesa and Montezuma counties. A male in the Colorado State University collection labeled "Ft. Collins, 11-1-24" is surely mislabeled.

thisbe Lucas. Alamosa, Baca, Bent, Crowley, El Paso, Huerfano, Kit Carson, Las Animas, Otero, and Prowers counties. Several rather exceptional records are from Boulder, Douglas, and Weld counties. All are males, one taken 5 July, the others in August; they may have been strays from breeding populations farther south.

Genus *Hemipepsis* Dahlbom

These wasps are superficially similar to species of *Pepsis* and, like them, are predators on mygalomorph spiders (Williams 1956).

ustulata ustulata Dahlbom. Archuleta, Baca, Bent, El Paso, Fremont, Huerfano, Las Animas, Mesa, Montezuma, and Otero counties.

Genus *Priocnessus* Banks

Compared to the previous 3 genera, these are smaller, slender-bodied wasps. The 2 species recorded from Colorado are rarely encountered, and nothing is known of their behavior. There are several records of an eastern species, *nebulosus* (Dahlbom), preying upon grass spiders of the genus *Agelenopsis*.

apache (Banks). Huerfano and Larimer counties. Townes (1957) recorded this species only from southern Arizona and Texas.

coloradensis (Banks). Boulder, Clear Creek, and Larimer counties.

Genus *Entypus* Dahlbom

These are wasps of moderate size, most of the species having orange wings and resembling small tarantula hawks. Several of the species have been found to prey on wolf spiders of the genus *Lycosa*, but so far as I am aware the nests have never been found.

aratus (Townes). Baca, Bent, and Otero counties.

austrinus austrinus (Banks). Bent, Boulder, Kiowa, Las Animas, and Otero counties.

fulvicornis (Cresson). Bent and Larimer counties.

texanus texanus (Cresson). Baca, Bent, Crowley, Huerfano, Kiowa, Larimer, Las Animas, Otero, Prowers, and Pueblo counties.

unifasciatus cressoni (Banks). Boulder, Clear Creek, Crowley, El Paso, Gunnison, Larimer, and Weld counties.

unifasciatus unifasciatus (Say). Yuma Co. An eastern subspecies.

Genus *Cryptocheilus* Panzer

The members of this genus closely resemble those of *Entypus*, but average smaller. As in *Entypus*, the females prey on wolf spiders of the genus *Lycosa*. The nests are multicellular and are dug from preexisting cavities in the soil.

attenuatus Banks. Boulder, Denver, Jefferson, Larimer, Mesa, and Otero counties.

hesperus (Banks). Crowley, Fremont, Lincoln, and Otero counties.

idoneum birkmanni Banks. Bent, Conejos, Huerfano, Kit Carson, Otero, Prowers, Saguache, Sedgwick, and Weld counties.

severini Banks. Baca, Bent, Boulder, Clear Creek, Crowley, Denver, Fremont, Huerfano, Larimer, Las Animas, Logan, Morgan, Otero, Prowers, Sedgwick, and Weld counties.

terminatus terminatus (Say). Archuleta, Bent, Boulder, Elbert, Garfield, Gunnison, Huerfano, Jefferson, Larimer, Las Animas, Mesa, Pitkin, and Weld counties.

Genus *Priocnemis* Schiodte

This is a large genus of small wasps that prey upon a great diversity of ground-dwelling spiders. Nests are multicellular and are often dug from preexisting cavities in the soil.

aequalis (Banks). Larimer Co.: a single female taken 21 km W of Livermore, at 2300 m elevation.
cornica (Say). Baca, Denver, Garfield, Kiowa, Larimer, Mesa, Teller, and Weld counties.
germana (Cresson). Delta and LaPlata counties.
kevini Wasbauer. Larimer Co.: 2 males taken in a malaise trap, 21 km W of Livermore, 2300 m.
minorata Banks. Larimer and El Paso counties.
navajo navajo Banks. Garfield, Larimer, Mesa, Mineral, and Routt counties.
notha notha (Cresson). Boulder, Garfield, Huerfano, LaPlata, Larimer, Morgan, and Routt counties. This and the preceding species are broadly sympatric and differ in details of the male terminalia; *navajo* in the past has been considered only subspecifically distinct from *notha*, but the two are clearly full species.
oregona Banks. Montezuma Co.: Mesa Verde National Park.
scitula relicta Banks. Larimer Co.: Fort Collins.

Genus *Caliadurgus* Pate

This is a small genus with a single uncommon species in Colorado. Prey is reported to be orb-weaving spiders that are flushed from their webs. The nest is a shallow burrow in the soil.

fasciatellus alienatus (Smith). Logan and Pueblo counties.
fasciatellus excoctus (Townes). Larimer Co.

Genus *Dipogon* Fox

Females of this genus have paired tufts of bristles on the maxillae (hence the name *Dipogon*, "two-beard"). They nest in hollow twigs and some will accept wooden trap nests. Cells are provisioned with small spiders of various genera, but most commonly crab-spiders (Thomisidae). Cells are separated by barriers of debris (bits of soil, wood, seeds, dead insects), the particles being carried with the help of the "beards." Members of this genus have rarely been collected in Colorado, being more partial to deciduous forests.

iracundus Townes. Boulder Co.: a single female taken by C.C. Lanham at Nederland, 2500 m.
lignicolus Evans. Larimer Co.: type locality and only records, 21 km W of Livermore, 2300 m.
sayi nigrior Townes. Larimer Co: a single female collected by David Leatherman at Estes Park, 2400 m. Townes (1957) recorded the species from Colorado, but without a specific locality.
sericeus Banks. Larimer Co.: a series of both sexes, taken in a malaise trap in Hewlett Gulch, 18 km NW Fort Collins, 1900 m.

Genus *Minagenia* Banks

Although Townes (1957) placed this genus in the subfamily Ceropalinae, I regard it as a probable derivative of *Priocnemis*. These are delicate wasps that do not build nests but oviposit directly upon lycosid spiders, which are left in place (Kaston 1959).

congrua (Cresson). Larimer Co.: Fort Collins.
montisdorsa Dreisbach. Bent Co.: Hasty.

Genus *Ageniella* Banks

This is the first of 3 genera of unusually slender body form, in which the females normally amputate some or all of the spiders' legs before transporting them to the nest. Species of *Ageniella* use a great variety of small spiders as prey, and so far as studied place them in short burrows dug from preexisting cavities in the soil. Sixteen species are reported from Colorado.

accepta (Cresson). Baca, Bent, Boulder, Huerfano, Larimer, Mesa, Moffat, Otero, Prowers, Pueblo, and Weld counties.
agenioides (Fox). Boulder and Larimer counties.
arapaho Evans. Larimer Co.: type locality and only records, 21 km W Livermore, 2300 m.
arcuata (Banks). Boulder, Larimer, Logan, and Montezuma counties.
arizonica arizonica (Banks). Otero Co.: 28 km S LaJunta.

conflicta Banks. Bent, Boulder, Garfield, Larimer, Montezuma, Morgan, and Weld counties.
cupida (Cresson). Larimer Co.: Poudre Canyon, 1600 m (Townes 1957).
euphorbiae (Viereck). Alamosa, Bent, Boulder, Conejos, Crowley, Huerfano, Larimer, Montezuma, Otero, Saguache, and Weld counties.
fulgifrons (Cresson). Larimer Co.: Fort Collins.
longula (Cresson). Larimer Co.: a single female taken 8 km NE of Livermore.
mintaka Brimley. Bent, Crowley, Delta, Huerfano, Larimer, Prowers, and Weld counties.
neglecta Banks. Boulder and Larimer counties.
placita sonorensis Townes. Delta Co. This is an unusual range extension for this species. A single female was collected by U.N. Lanham 5 mi N of Delta, 30 June 1938.
reynoldsi (Banks). Bent and Las Animas counties.
rufescens (Banks). Boulder and Larimer counties.
semitincta (Banks). Bent, Boulder, Huerfano, Larimer, Mesa, Montezuma, and Otero counties.

Genus *Phanagenia* Banks

This is a small genus of wasps in which the females utilize spiders of several kinds and place their paralyzed prey in oval mud cells built beneath stones or logs.

bombycina (Cresson). Boulder, Larimer, and Montezuma counties.

Genus *Auplopus* Spinola

This is a large genus of worldwide distribution. The females make mud cells in protected places by carrying water from pools or puddles and making pellets from dry soil; the pellets are carried in the mouthparts and applied to the nest cells by use of the tip of the abdomen as a trowel. Spiders of diverse groups are used as prey.

architectus architectus (Say). Arapahoe, Boulder, Delta, Fremont, Jefferson, Larimer, Montezuma, and Weld counties.
caerulescens subcorticalis (Walsh). Boulder Co.
mellipes variitarsatus (Dalla Torre). Larimer Co.: Fort Collins.
nigrellus (Banks). Bent, Boulder, Chaffee, Denver, Douglas, El Paso, and Larimer counties.

SUBFAMILY POMPILINAE

Genus *Aporus* Spinola

Members of this genus prey on trap-door spiders (Ctenizidae) using the spider's burrow as a nest.

luxus (Banks). Montezuma Co.: several males taken in a malaise trap at Arriola by T. Marquardt. This is primarily a species of the western coastal states.

Genus *Psorthaspis* Banks

This is another genus of predators on trapdoor spiders. The species show strong sexual dimorphism, the females of our species being patterned with orange, similar to many Mutillidae, while the males are all black, a presumed example of Mullerian mimicry.

nigriceps (Banks). Montrose Co.: Uravan. A species of the deep Southwest.
sanguinea (Smith). Baca and Otero counties.

Genus *Evagetes* Lepeletier

Members of this genus are nest parasites of other Pompilidae. Females seek out and dig into nests of other spider wasps, destroy the egg, and lay an egg of their own on the spider.

asignus Dreisbach. Alamosa, Bent, Huerfano, Larimer, Prowers, Weld, and Yuma counties.
calefactus Evans. Larimer Co. A single female of this evidently rare species was taken by the author 10 km E of Livermore PO on 9 August 1996 on foliage of *Helianthus annuus*. This is the first Colorado record of a species previously known from California, Arizona, Texas, and (questionably) Montana.
crassicornis consimilis (Banks). Boulder, Larimer, Mesa, Mineral, Park, and Teller counties.
crassicornis crassicornis (Shuckard). Larimer Co.: Fort Collins.
hyacinthinus (Cresson). Alamosa, Baca, Boulder, Conejos, Gilpin, Huerfano, Jefferson, Larimer, Mesa, Otero, and Weld counties.
ingenuus (Cresson). Alamosa, Bent, El Paso, Larimer, Morgan, Otero, Prowers, and Yuma counties.

mohave (Banks). Alamosa, Baca, Bent, Boulder, Cheyenne, Huerfano, Larimer, Moffat, Montezuma, and Weld counties.

padrinus padrinus (Viereck). Bent, Boulder, Delta, Jefferson, Larimer, Mesa, Moffat, Montezuma, Routt, Washington, and Weld counties.

parvus (Cresson). Baca, Bent, Boulder, Delta, Douglas, Eagle, El Paso, Jackson, Jefferson, Larimer, Moffat, Montezuma, Morgan, Otero, Routt, Washington, and Weld counties.

subangulatus (Banks). Boulder, Huerfano, Jefferson, Larimer, Mesa, Moffat, Montezuma, Park, Pueblo, and Weld counties.

Genus *Agenioideus* Ashmead

These are small wasps of delicate build, nesting (so far as known) from inside crevices in the soil.

biedermani (Banks). Bent, Larimer, and Weld counties.

birkmanni (Banks). Larimer, Mesa, and Otero counties.

humilis (Cresson). Alamosa, Boulder, El Paso, and Larimer counties. This is a predator on orb-weaving spiders, often around buildings.

Genus *Sericopompilus* Howard

This is a small genus of slender wasps that prey on diverse spiders and nest in the soil, usually from the side of a rodent burrow or the burrow of another wasp.

angustatus (Cresson). Bent, Boulder, El Paso, Prowers, Weld, and Yuma counties.

apicalis (Say). Baca, Bent, and Prowers counties.

neotropicalis (Cameron). Otero Co.: Hawley.

Genus *Episyron* Schiodte

These small wasps prey exclusively on orb-weaving spiders (Araneidae), which they flush from their webs, sting, and carry to a simple nest dug in the soil. So rapid are their actions that George and Elizabeth Peckham (1898) called 1 species "the tornado wasp."

biguttatus biguttatus (Fabricius). Baca, Bent, Larimer, and Otero counties.

biguttatus californicus (Banks). Alamosa, Chaffee, Huerfano, Larimer, and Montezuma counties.

oregon Evans. Grand and Larimer counties.

quinquenotatus hurdi Evans. Alamosa, Conejos, Huerfano, Larimer, Mesa, Park, Saguache, and Weld counties.

quinquenotatus quinquenotatus (Say). Alamosa, Boulder, El Paso, Larimer, Saguache, and Weld counties.

snowi (Viereck). Baca, Bent, Boulder, Crowley, Delta, El Paso, Huerfano, Kiowa, Larimer, Las Animas, Mesa, Montezuma, Prowers, and Weld counties.

Genus *Poecilopompilus* Howard

These are moderate-sized wasps that are frequently banded with black and yellow, much like social wasps of the genus *Polistes*. Like members of the preceding genus, they are specialists on orb-weaving spiders and nest in simple burrows in the soil.

algidus coquilletti (Provancher). Mesa Co.: Colorado National Monument.

algidus willistoni (Patton). Alamosa, Baca, Bent, Crowley, Larimer, Las Animas, Montezuma, Prowers, and Weld counties.

interruptus interruptus (Say). Baca, Bent, Kiowa, Las Animas, Montezuma, Otero, Prowers, Pueblo, and Weld counties.

Genus *Tachypompilus* Ashmead

These are large wasps of mostly reddish brown coloration. They prey largely on wolf spiders (*Lycosa* and *Dolomedes*) and place their paralyzed prey in shallow burrows in sandy or powdery soil, often close to buildings.

ferrugineus ferrugineus (Say). Arapahoe, Boulder, Larimer, and Jefferson counties.

unicolor cerinus Evans. Bent, Crowley, and Otero counties.

unicolor unicolor (Banks). Larimer Co.: 32 km N Fort Collins. This western subspecies has also been taken twice in Wyoming: Green River and 30 miles NE of Laramie.

Genus *Anoplius* Dufour

Subgenus *Notiochares* Banks

This is a small subgenus of mostly black or bluish wasps of moderate size. It is primarily a neotropical group, with 1 species that is occasionally taken in Colorado. The prey consists of wolf spiders that are most often taken in tall grasses in wet places.

lepidus atramentarius (Dahlbom). Baca, Larimer, and Prowers counties.

Subgenus *Lophopompilus* Radoszkowski

This is another small subgenus of rather large wasps, in this case Holarctic in distribution. Relatively large spiders of several families are used as prey. Nests are dug from flat soil or from the sides of preexisting holes.

aethiops (Cresson). Arapahoe, Archuleta, Bent, Boulder, Conejos, Crowley, Denver, Fremont, Huerfano, Jefferson, Larimer, Las Animas, Montrose, Otero, Saguache, Weld, and Yuma counties.

atrox (Dahlbom). Boulder and Larimer counties.

cleora (Banks). Alamosa, Baca, Delta, Mesa, Moffat, Prowers, Weld, and Yuma counties. Largely confined to the vicinity of streams and lakes.

Subgenus *Arachnophroctonus* Howard

Species of this subgenus are inhabitants of open country where the soil is reasonably friable. Simple nests are dug in the soil and provisioned primarily with wolf spiders (Lycosidae).

acapulcoensis (Cameron). Baca, Bent, Cheyenne, Otero, Prowers, and Pueblo counties.

americanus ambiguus (Dahlbom). Mesa Co.

nigritus (Dahlbom). Alamosa, Baca, Bent, Boulder, Cheyenne, Conejos, Costilla, Crowley, Delta, Denver, Douglas, Elbert, El Paso, Garfield, Huerfano, Larimer, Las Animas, Logan, Mesa, Morgan, Otero, Prowers, Weld, and Yuma counties. This species has been called *relativus* (Fox) for many years.

semicinctus (Dahlbom). Alamosa, Baca, Bent, Conejos, Costilla, El Paso, Huerfano, Kiowa, Las Animas, Morgan, Otero, Prowers, Weld, and Yuma counties. This species has been called *marginalis* (Banks) for many years.

semirufus (Cresson). Baca, Bent, Larimer, Mesa, and Weld counties.

Subgenus *Pompilinus* Ashmead

This subgenus is closely similar to the preceding, but the species are smaller in size. Wolf spiders are the most common prey, but a variety of other ground-dwelling spiders are also used. Fifteen species are reported from Colorado.

brevihirta (Banks). Alamosa, Bent, El Paso, Prowers, Saguache, and Weld counties. An inhabitant of sand dunes.

clystera (Banks). Archuleta, Baca, Bent, Boulder, Crowley, Delta, Gilpin, Gunnison, Kiowa, Larimer, Mesa, and Otero counties.

cylindricus (Cresson). Prowers Co.: Carlton.

estellina (Banks). Delta and Larimer counties.

fraternus (Banks). Kiowa and Logan counties.

insolens (Banks). Alamosa, Bent, Boulder, Conejos, Delta, Gunnison, Huerfano, Larimer, Mesa, Moffat, Morgan, Otero, Prowers, Pueblo, Washington, and Weld counties.

leona (Cameron). Larimer Co., 8–10 km E of Livermore PO: 3 females taken 4–5 August 1994 on *Euphorbia marginata* and a male taken 20 August 1996 on foliage of *Helianthus annuus*. First Colorado record of a species described from Mexico and reported from Texas, New Mexico, and Arizona.

marginatus (Say). Cheyenne, Costilla, El Paso, Kiowa, Larimer, Moffat, Morgan, Sedgwick, Weld, and Yuma counties.

percitus Evans. Bent, Boulder, Douglas, Eagle, Jefferson, Larimer, Morgan, and Prowers counties.

rectangularis rectangularis (Dreisbach). Larimer and Yuma counties.

splendens (Dreisbach). Bent, Costilla, El Paso, Larimer, Lincoln, Logan, Morgan, Otero, Prowers, and Weld counties.

subcylindricus (Banks). Arapahoe, Archuleta, Baca, Bent, Boulder, Cheyenne, Delta, Huerfano, Larimer, Lincoln, Otero, and Phillips counties.

subtruncatus (Dreisbach). Bent, Elbert, Larimer, Otero, and Weld counties.

tenebrosus (Cresson). Boulder, Clear Creek, Douglas, Eagle, Gilpin, Jackson, Jefferson, Larimer, Mesa, Mineral, Moffat, Montezuma, Montrose, Morgan, Routt, and Teller counties.

truncatus (Dreisbach). Bent, Larimer, Prowers, and Weld counties.

Subgenus *Anoplius* Dufour

These are small black or bluish wasps that nest primarily in niches, such as under stones or logs. Prey consists of various ground-dwelling spiders.

dreisbachi Evans. Archuleta, Boulder, Elbert, El Paso, Fremont, Huerfano, Larimer, Mesa, Morgan, Otero, Sedgwick, and Weld counties.

hispidulus Dreisbach. Elbert Co.: Running Creek Field Station, 2120 m.

illinoensis (Robertson). Boulder, Delta, Garfield, Larimer, and Weld counties.

imbellis Banks. Boulder, Jackson, Larimer, Mesa, and Mineral counties.

ithaca (Banks). Larimer Co. Nests along streams, building short galleries among stones.

nigerrimus (Scopoli). Larimer Co.: Stevens Gulch, 22 km NW Fort Collins, 2200 m.

papago Banks. Bent, Garfield, Kiowa, and Otero counties.

toluca (Cameron). Bent and Larimer counties.

virginiensis (Cresson). Recorded from Colorado, without further data, by Evans (1951).

Genus *Hesperopompilus* Evans

This is a small genus of rare, little-studied species, most of them confined to the Southwest or Mexico.

orophilus (Evans). Fremont and Larimer counties.

Genus *Arachnospila* Kincaid

Subgenus *Ammosphex* Wilcke

These are small wasps more often taken in wooded areas than on the plains. The prey consists primarily of small wolf spiders. This and the following 2 subgenera are Holarctic in distribution.

angularis angularis (Banks). Boulder, Delta, Jefferson, Larimer, Las Animas, Mesa, Teller, and Weld counties.

anomala anomala (Dreisbach). Bent, Costilla, Douglas, Larimer, Mesa, Montezuma, Morgan, and Pueblo counties.

dakota (Dreisbach). Boulder, Larimer, and Teller counties.

imbecilla imbecilla (Banks). Chaffee, Lake, Larimer, and Teller counties.

luctuosa (Cresson). Boulder, Conejos, Custer, Lake, Larimer, Montezuma, Park, and Summit counties.

michiganensis (Dreisbach). Grand, Jefferson, and Larimer counties.

occidentalis (Dreisbach). Adams, Boulder, Costilla, Denver, Elbert, El Paso, Larimer, Mesa, Mineral, Park, Rio Blanco, and Weld counties.

parvula (Banks). Alamosa, Boulder, Huerfano, Jackson, Larimer, and Teller counties.

silvivaga (Evans). Alamosa, Boulder, and Larimer counties.

Subgenus *Arachnospila* Kincaid

These are black wasps, averaging larger than those of the preceding subgenus. Females prey upon various ground-dwelling spiders and make simple nests in friable soil.

arcta (Cresson). Alamosa, Boulder, Conejos, Denver, El Paso, Grand, Gunnison, Hinsdale, Huerfano, Larimer, Mesa, Moffat, Montrose, Park, San Miguel, and Teller counties.

fumipennis eureka (Banks). Alamosa, Arapahoe, Boulder, Gilpin, Jefferson, Larimer, Ouray, and Routt counties.

scelesta (Cresson). Alamosa, Arapahoe, Bent, Boulder, Chaffee, Conejos, Delta, Denver, Eagle, El Paso, Gilpin, Huerfano, Jackson, Jefferson, Kiowa, Larimer, Las Animas, Lincoln, Mesa, Moffat, Otero, Park, Saguache, Teller, Weld, and Yuma counties.

Subgenus *Anoplochares* Banks

Nothing is known of the behavior of the single species of this subgenus occurring in Colorado. A European species is known to attack burrowing wolf spiders, using the spider's burrow as a nest.

apicata (Provancher). Bent, Boulder, Garfield, Gilpin, Jefferson, Larimer, and Weld counties.

Genus *Aporinellus* Banks

These are minute wasps, all species extensively patterned with pale pubescence. Records indicate that jumping spiders (Salticidae) are the usual prey. Nests are simple burrows in the ground.

basalis Banks. Alamosa, Bent, Delta, Jackson, Larimer, Otero, and Weld counties.

completus Banks. Bent, Chaffee, Delta, Huerfano, Jackson, Larimer, Mesa, Montezuma, Washington, and Weld counties.

medianus Banks. Alamosa, Bent, Delta, Jefferson, Larimer, Teller, and Weld counties.

taeniolatus rufus Banks. Baca, Bent, Boulder, Larimer, Teller, and Weld counties. Probably no more than a color form of the following.

taeniolatus taeniolatus (Dalla Torre). Bent, Boulder, Delta, Larimer, and Pueblo counties.

unionis (Dalla Torre). Bent, Boulder, Delta, Douglas, Huerfano, Jefferson, Larimer, Mesa, Moffat, Montezuma, Otero, and Weld counties. For many years this species was called *fasciatus* (Smith).

yucatanensis (Cameron). Bent, Boulder, Delta, Douglas, Huerfano, Larimer, Mesa, Moffat, Montezuma, Otero, and Weld counties.

Genus *Paracyphononyx* Gribodo

These large, black wasps do not build nests but attack wolf spiders in their burrows, the wasp larva developing on the spider as a parasitoid.

funereus (Lepeletier). Baca, Bent, Boulder, Delta, El Paso, Huerfano, Larimer, Las Animas, Mesa, Montezuma, Otero, and Prowers counties.

Subfamily Ceropalinae

Genus *Ceropales* Latreille

Members of this genus are parasites of other Pompilidae. Females are attracted to nesting females, then slip in and lay an egg in the book lungs of the spider. The *Ceropales* egg hatches before that of the host and the larva consumes the host egg and then the spider.

brevicornis Patton. Bent, Boulder, El Paso, Kiowa, Larimer, Otero, Prowers, and Weld counties.

elegans aquilonia Townes. Larimer and Weld counties.

elegans elegans Cresson. Bent, Larimer, Prowers, and Weld counties.

maculata fraterna Smith. Boulder, Grand, Huerfano, Jackson, Jefferson, LaPlata, Larimer, and Montezuma counties.

nigripes Cresson. Baca, Bent, Crowley, El Paso, Kiowa, Larimer, Las Animas, Logan, Morgan, Otero, and Prowers counties.

robinsonii robinsonii Cresson. Larimer Co.: 21 km W Livermore, 2300 m.

robinsonii stigmatica Banks. Larimer Co. Taken at the same locality as the preceding and doubtless no more than a color form.

rugata Townes. Bent, Delta, Huerfano, Larimer, Montezuma, Otero, and Weld counties.

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GROWTH AND SURVIVORSHIP OF FREMONT COTTONWOOD, GOODDING WILLOW, AND SALT CEDAR SEEDLINGS AFTER LARGE FLOODS IN CENTRAL ARIZONA

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Abstract.—During winter 1993, Arizona experienced regional river flooding. Floodwaters at the Hassayampa River eroded floodplains and created a 50-m-wide scour zone available for colonization by pioneer plant species. The slow rate and long duration of the floodwater recession allowed establishment of spring-germinating native trees (mainly Fremont cottonwood [*Populus fremontii*] and Goodding willow [*Salix gooddingii*] as well as summer-germinating species including the introduced salt cedar (*Tamarix chinensis* and related species). Goodding willow and Fremont cottonwood seedlings showed zonation in the floodplain, while salt cedar was equally abundant in zones with saturated and dry surface soils. Floodplain elevation (and soil moisture) influenced shoot growth rate to different degrees among the 3 species. For example, Goodding willow seedlings were significantly taller in areas with saturated soils than dry surface soils; Fremont cottonwoods were taller in the dry surface soil areas; and salt cedar were equally short in both soil moisture zones. Other factors that differentially influenced abundance or growth rates included competition with herbaceous species (*Melilotus* spp., an introduced plant, locally preempted salt cedar establishment) and herbivory (selective browsing by livestock at 1 river site reduced the natural height advantage of the native tree species). I draw on the results of this descriptive field study to suggest ways in which stream flows and floodplain land use can be managed to restore ecological conditions that favor native tree species over the introduced and widespread salt cedar.

Key words: riparian habitats, floods, Populus fremontii, Salix gooddingii, Tamarix chinensis.

Fremont cottonwood *(Populus fremontii)* and Goodding willow *(Salix gooddingii)* are pioneer species that establish episodically after winter/spring flood flows along rivers of the desert Southwest (Stromberg et al. 1991, Everitt 1995). Winter/spring floods scour competing vegetation, deposit and rework alluvial sediments, and provide supplemental moisture during the short period in spring during which the seeds disperse and germinate. Salt cedar (*Tamarix chinensis* and related species), an invasive riparian shrubby tree native to Eurasia, also is adapted to establish after flood disturbance but establishes more opportunistically than Fremont cottonwood and Goodding willow (Brock 1994). Salt cedar initiates seed dispersal later in the season but disperses its seeds over a longer period of time (Warren and Turner 1975). Thus, depending in part on timing and duration, floods may either preclude or enhance salt cedar establishment. For example, salt cedar seedlings were scarce after a small spring flood in the Hassayampa River in 1991 because the narrow band of germination space created by the rapidly receding floodwaters was colonized by Fremont cottonwood, Goodding willow, and herbaceous vegetation (Stromberg et al. 1993). Larger floods of longer duration, in contrast, have been observed to facilitate establishment of various species of *Tamarix* (Stevens and Waring 1985, Ohmart et al. 1988, Griffin et al. 1989).

During winter 1993, Arizona experienced regional river flooding. Although instantaneous peaks were on par with other recent large floods, the 1993 event ranked as one of the most severe in state history when collectively considering magnitude, duration, and volume (House 1995). The 1993 floods caused much geomorphic and vegetational change, including channel widening (Huckleberry 1994) and mass wasting of floodplains supporting velvet mesquite *(Prosopis velutina)* woodland and Fremont cottonwood–Goodding willow forest. The floods also created extensive habitat for riverine marshland and young stands of cottonwood and willow (Stromberg et al. 1997). I undertook this study with the objective of determining how abundance, distribution, growth, and survivorship of seedlings and vegetative sprouts of Fremont cottonwood, Goodding willow, salt cedar, and various shrubs were influenced by the 1993 floods, and by hydrologic events in subsequent years.

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STUDY SITES

Study sites are located on perennial reaches of 3 central Arizona Sonoran rivers. One site is in the Arizona Nature Conservancy's Hassayampa River Preserve in northwest Maricopa County (elevation ca 600 m). The Hassayampa River has a mean annual flow rate of 0.5 m^3s^{-1} at the Morristown gage (USGS #9516500), located about 4 km downstream of the preserve. Surface sediments are predominantly sand. Surface water has an electrical conductivity of 600–700 uS/cm. The area was grazed by cattle prior to 1987, but the main land use at the preserve is now ecotourism. The Santa Maria River study site is in the Alamo Lake Wildlife Management Area (elevation 365 m), in Mohave and La Paz counties, and is grazed by feral burro and trespass cattle. Mean annual flow rate of the Santa Maria is 2 m^3s^{-1} at the Bagdad gage (USGS #9424900), located about 5 km upstream of the study reach. The Date Creek site is on Arizona State land, leased by Date Creek Ranch (elevation 880 m). Date Creek is a tributary to the Santa Maria River and is not gaged. The Date Creek floodplain is grazed by cattle from November to March.

Floodplains of all 3 rivers are vegetated primarily by Fremont cottonwood–Goodding willow forests, velvet mesquite woodlands, burro brush *(Hymenoclea monogyra)* scrublands, and seep willow *(Baccharis salicifolia)* stands (Brown 1982). Other woody species include Arizona ash (*Fraxinus velutina*), Bonpland willow (*Salix bonplandiana*), coyote willow (*Salix exigua*), arrow weed (*Tessaria sericea*), and screwbean mesquite (*Prosopis pubescens*). Salt cedar had lower density than Fremont cottonwood or willows at study sites at all 3 rivers (Table 1), based on sampling of saplings and trees (stems >2 cm at breast height) in 1994 with the point-quarter method (20 points per river).

TABLE 1. Density (stems/ha of stems >2 cm) of native and exotic pioneer species in forest stands at 3 central Arizona study rivers.

	Fremont cottonwood	Goodding and Bonpland willows	Salt cedar
Hassayampa River	287	412	45
Santa Maria River	312	416	195
Date Creek	45	60	5

METHODS

At the Hassayampa River, data were collected at a total of 100 permanent plots distributed along 8 transects established at the preserve in 1987. Plots were located at known distances along the transect line, allowing for reestablishment of plot markers (rebar) that were removed or buried during floods. Floodplain topography and changes in plot surface elevation due to sediment deposition and scour were determined based on repeat cross-sectional surveys of the Hassayampa River transects (Stromberg et al. 1997). Plots (1 × 1 m) were sampled for density and height of woody seedlings and vegetative stem sprouts 3–5 times per year during 1993, 1994, and 1995. Shoot height was measured for the tallest individual per species per plot. Plants were assumed dead if absent from plots, although live root or stem fragments may have been dispersed from plots in floodwaters. The nonparametric Kruskal-Wallis test was used to test for significant differences in survivorship of the 1995 flood between 1993 seedling cohorts of Fremont cottonwood, Goodding willow, and salt cedar. Spearman rank correlation analysis was used to determine whether seedling survivorship of the 1995 flood (using pooled values for all 3 tree species) varied with distance from the 1993 channel edge. SPSS for Windows was used for all statistical analyses.

At all 3 rivers, 50 randomly located 1 × 1-m plots were sampled in June and October of 1994 within 1 or 2 soil moisture zones in the scoured flood channel. Fifty plots were in a zone with saturated surface soils or shallow standing water (<3 cm), and 50 were in a zone with slightly higher surface elevation (10–30 cm higher) and dry or damp surface soils (as of June 1994). At Date Creek the saturated soil zone was not extensive, and plots were sampled only in the dry surface zone. Woody seedlings in the plots were sampled for density, and for height and browse status (browsed or unbrowsed) of the tallest individual per species. Plants were classified as browsed if any of the shoots had been eaten. If there were <20 individuals of Fremont cottonwood, Goodding willow, or salt cedar in the 50 plots, stem height and browse status were measured in additional random plots to increase sample size to 20 individuals per species per zone. Herbaceous cover, by species, was visually estimated in the plots using gridded plot frames to reduce sampling error.

One-way analysis of variance (ANOVA) with post-hoc Sheffe's multiple comparison test was used to detect statistical difference in stem density ($n = 50$ plots) and stem height ($n = 20$ individuals per species) between Fremont cottonwood, Goodding willow, and salt cedar within zones of each river. Independent sample Student's t tests were used to compare density ($n = 50$ plots) and stem height ($n = 20$) of each species between the saturated and dry surface zones of the Hassayampa and Santa Maria rivers. Additionally, plots within the dry surface zone at the Hassayampa River were subsequently divided into those with >50% and <50% cover of sweet clover (*Melilotus albus* and *M. officinalis*), and densities of salt cedar and Fremont cottonwood were compared between the 2 groups with Student's t tests.

RESULTS

Surface Flow

The 1993 flood in the Hassayampa River had a 25-yr recurrence interval, with instantaneous flow rates peaking at 745 m^{3}s^{-1} on 8 January 1993. This was followed by flood peaks of 218 m^{3}s^{-1} on 17 January, 328 m^{3}s^{-1} on 9 February, and 439 m^{3}s^{-1} on 20 February. Surface flow was above average during spring and summer of 1993 and was present through August at the Morristown gage, located in a frequently dry reach of the Hassayampa River (Fig. 1). Floodwaters in 1993 had an estimated depth of 3.0 m on low floodplain terraces and a velocity of 2.1 m s^{-1}. Floodwaters enlarged the channel from about 3 to 50 m wide and caused a net lowering of the floodplain surface. Throughout 1994, instantaneous flow rates never exceeded 2 m^{3}s^{-1}. During 1995, instantaneous flow rates peaked at 566 m^{3}s^{-1} (15- to 20-yr recurrence interval) in February. Flows remained high in spring and summer of 1995 but diminished more rapidly than in 1993. Surface flow was present at the Morristown gage through June 1995. The 1995 floods deposited sediment on large portions of the floodplain, raising the elevation of the scour zone relative to 1993 (Stromberg et al. 1997). The Santa Maria also had large flood peaks. Instantaneous discharges in the Santa Maria peaked in 1993 at 347 m^{3}s^{-1} on 8 January, 440 m^{3}s^{-1} on 9 February, and 356 m^{3}s^{-1} on 20 February.

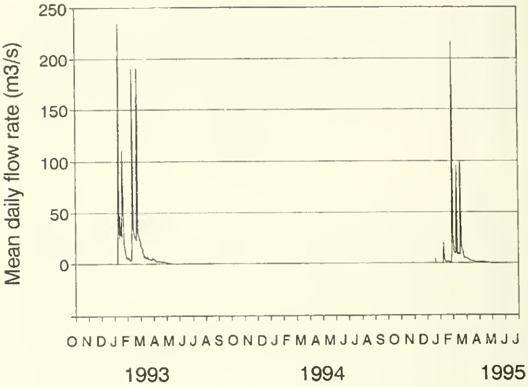

Fig. 1. Mean daily flows in the Hassayampa River at the Morristown gage during water years 1993, 1994, and 1995.

1993 Seedling Cohort

TEMPORAL AND SPATIAL DISTRIBUTION.—As the Hassayampa River floodwaters receded in 1993, woody plants germinated in exposed moist soils in the following sequence: Fremont cottonwood (March–April), Goodding willow (April–May), salt cedar (May–September), arrow weed (July–September), and seep willow (July–September; Fig. 2). Trace amounts (<0.01 stem/m^2) of Bonpland willow were recorded from Date Creek (data not shown), but this species was not present at the Hassayampa River site.

Woody seedlings showed zonation in the floodplains of the Hassayampa and Santa Maria rivers (Table 2). Fremont cottonwood was significantly more abundant in dry surface zones, while Goodding willow, coyote willow, and arrow weed were significantly more abundant in zones with saturated soils. Salt cedar and seep willow were equally abundant in both zones. Within the dry surface zone at the Hassayampa River, however, salt cedar seedlings varied significantly (t test, $P < 0.05$) in density depending on cover of yellow and white sweet clover (Fig. 3). Salt cedar seedlings were nearly absent in plots with high sweet clover cover but averaged 15 stems/m^2 in plots with little

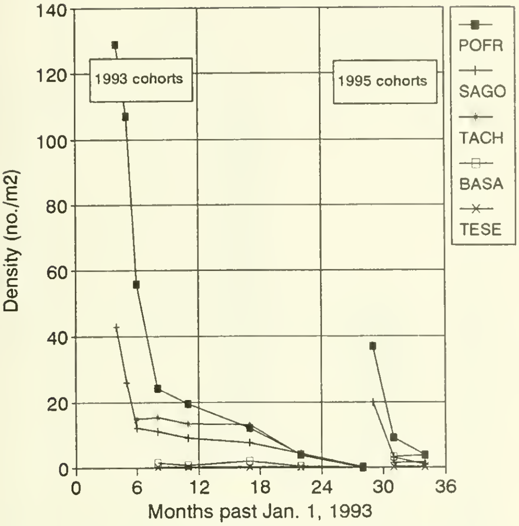

Fig. 2. Density of woody seedlings established after floods in 1993 and 1995 in the Hassayampa River (POFR = *Populus fremontii*, SAGO = *Salix gooddingii*, TACH = *Tamarix chinensis*, BASA = *Baccharis salicifolia*, TESE = *Tessaria sericea*).

or no sweet clover. Fremont cottonwood seedlings were equally dense in plots with low and high values for sweet clover cover. Yellow and white sweet clover are introduced biennials and had high cover in 1993 and 1994 in the dry surface zone of the Hassayampa River Preserve.

ABUNDANCE AND SURVIVORSHIP.—At the Hassayampa River, Fremont cottonwood was the most abundant species in the dry soil zone after 1 growing season, and Goodding willow was most abundant in the saturated soil zone (Fig. 4). After 2 growing seasons, Fremont cottonwood and salt cedar seedlings had declined to approximately equal densities in the dry soil zone, as had Goodding willow and salt cedar in the saturated soil zone. At the Santa Maria River, Fremont cottonwood and Goodding willow seedlings showed trends of being more abundant in the dry surface and saturated soil zones, respectively. Salt cedar seedlings, however, were significantly more abundant than either native tree species in both zones at the Santa Maria River after a single growing season; and densities did not differ significantly between species after 2 growing seasons. Seedling densities did not differ significantly between species at Date Creek.

At the end of the 1993 growing season (November), Fremont cottonwood seedlings had a mean density of 20 stems/m^2 in the Hassayampa River flood channel as a whole, followed by salt cedar (13 stems) and Goodding willow (9 stems). Values had declined to about 4 stems/m^2 for each species by October 1994. The 1995 floods caused high mortality of these remaining 1993 seedling cohorts. In Hassayampa River study plots, Fremont cottonwood and Goodding willow seedlings had 96% mortality, and salt cedar had 100% mortality. Between-species differences in survivorship were not statistically significant at $P < 0.05$. However, there was a significant correlation ($r = 0.50$; $P < 0.05$; $n = 28$) between woody seedling survivorship and distance of the plot from the edge of the channel as of 1993. Fremont cottonwoods and Goodding willows that did survive were mainly in narrow bands along the edge of the scour zone, with some surviving despite deposition of up to 1 m of sediment.

GROWTH RATES AND BROWSE RATES.—On average in the Hassayampa River floodplain, seedlings of native tree species (Goodding willow and Fremont cottonwood) were taller than salt cedar and native shrub species (seep willow and arrow weed; Fig. 5). Among tree species, Goodding willows were significantly taller than Fremont cottonwood and salt cedar during their 1st and 2nd growing seasons in the saturated soil zones at the Hassayampa and Santa Maria rivers (Fig. 6). In dry surface zones at river sites, the 3 species did not differ significantly in height after 1 growing season. After 2 growing seasons native tree species were significantly taller than salt cedar in the dry surface zone at the Hassayampa and Santa Maria rivers but not at Date Creek. Date Creek was the only study site with high rates of browse by livestock, with 89% of the Fremont cottonwood seedlings and 5% of the salt cedar seedlings classified as browsed as of June 1994. In most cases browsing resulted in loss of the terminal shoot. Browse rates were <5% per species at the other 2 rivers.

Fremont cottonwoods were significantly taller in the dry surface zone than in the saturated soil zones at both the Hassayampa and Santa Maria rivers, after 1 and 2 growing seasons (Table 3). In contrast, Goodding willows tended to be taller in the saturated soil zone, but differences between zones were significant only at the Hassayampa River during the 1st growing

TABLE 2. Stem density (no./m^2) of 1993 seedling cohorts of *Populus fremontii* (POFR), *Salix gooddingii* (SAGO), *Tamarix chinensis* (TACH), *Baccharis salicifolia* (BASA), *Tessaria sericea* (TESE), and *Salix exigua* (SAEX) at the Hassayampa River Preserve (HR), Santa Maria River (SM), and Date Creek (DC), by moisture zone. Values shown are means ± standard errors. "t" indicates values less than 0.1.

	June 1994						October 1994					
	POFR	SAGO	TACH	BASA	TESE	SAEX	POFR	SAGO	TACH	BASA	TESE	SAEX
Dry surface: HR	38.3 ± 5.9*	3.2 ± 0.6	11.4 ± 4.4	1.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	10.2 ± 4.4*	0.4 ± 0.2	7.8 ± 1.7	0.4 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Saturated soils: HR	1.2 ± 0.3	38.1 ± 5.7*	10.8 ± 7.5	0.9 ± 0.4	0.3 ± 0.1*	0.0 ± 0.0	1.1 ± 0.4	18.5 ± 5.7*	9.6 ± 2.6	0.3 ± 0.1	0.3 ± 0.1*	0.0 ± 0.0
Dry surface: SM	5.9 ± 0.6*	0.3 ± 0.2	34.3 ± 5.9	1.3 ± 0.4	0.1 ± 0.1	0.0 ± 0.0	2.5 ± 0.7*	0.0 ± 0.0	5.1 ± 1.4	0.3 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Saturated soils: SM	0.1 ± 0.1	3.7 ± 0.5*	27.6 ± 4.7	1.3 ± 0.7	5.2 ± 0.7*	0.3 ± 0.0*	0.1 ± 0.1	2.6 ± 1.2*	7.4 ± 2.4	0.1 ± 0.1	1.9 ± 0.6*	0.1 ± 0.1
Dry surface: DC	2.3 ± 0.6	0.2 ± 0.1	0.9 ± 0.3	0.6 ± 0.2	0.0 ± 0.0	t	1.0 ± 0.4	0.0 ± 0.0	0.8 ± 0.3	0.4 ± 0.1	0.0 ± 0.0	t

*Significant difference between moisture zones at $P < 0.05$

TABLE 3. Stem height for 1993 seedling cohorts of *Populus fremontii* (POFR), *Salix gooddingii* (SAGO), and *Tamarix chinensis* (TACH) at the Hassayampa River Preserve (HR), Santa Maria River (SM), and Date Creek (DC), by moisture zone, after 1 and 2 growing seasons. Values shown are means ± standard errors.

	One growing season[a]			Two growing seasons[b]		
	POFR	SAGO	TACH	POFR	SAGO	TACH
Dry surface: HR	78 ± 9*	77 ± 8	52 ± 5	128 ± 8*	125 ± 11	53 ± 7
Saturated soils: HR	45 ± 6	103 ± 9*	53 ± 7	71 ± 6	149 ± 11	45 ± 5
Dry surface: SM	60 ± 6*	60 ± 8	40 ± 6	141 ± 8*	—	74 ± 6
Saturated soils: SM	35 ± 5	80 ± 8	41 ± 5	67 ± 8	116 ± 12	71 ± 11
Dry surface: DC	46 ± 6	66 ± 9	47 ± 6	55 ± 5	—	45 ± 4

[a] Measured in June 1994
[b] Measured in October 1994
*Significant difference between moisture zones at $P < 0.01$

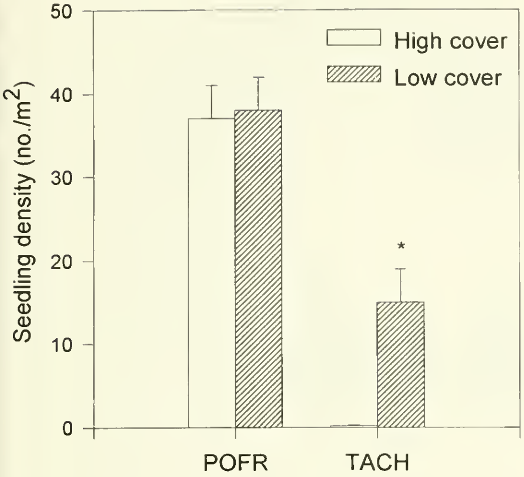

Fig. 3. Stem density of 1993 seedling cohorts of *Populus fremontii* (POFR) and *Tamarix chinensis* (TACH) in plots with <50% cover of *Melilotus* species (n = 32; mean cover of 76 ± 7) and >50% (n = 18; mean cover or 5 ± 1), as of June 1994. Values shown are means and standard error bars.

season. Salt cedar height did not differ significantly between zones.

1995 Seedling Cohort

Seedlings of all 3 tree species again germinated in 1995 in the moist, scoured zone exposed by the slowly receding floodwaters. In the Hassayampa River floodplain, densities of the 1995 seedling cohorts ranged among the 3 species from 1 to 4 stems/m^2 as of October 1995, compared to 9–20 stems/m^2 for the 1993 cohorts as of November 1993. Dry surface soils were relatively more abundant and saturated soils less abundant in 1995 than 1993, partly due to floodplain aggradation in 1995. Fremont cottonwood seedlings were the most abundant of the 3 tree species in 1995 and outnumbered salt cedar by a ratio of about 2:1 as of October 1995. Seedlings of all 3 species tended to have shorter stems in 1995 than in 1993, but the difference between years was significant at $P < 0.05$ only for Goodding willow (Fig. 7).

Densities of vegetative sprouts were greater in 1995 than during 1993. There were 0.25, 0.36, and 0.02 stems/m^2 for Fremont cottonwood, Goodding willow, and salt cedar, respectively, as of October 1995, compared to <0.01 stems per species in November 1993. Many of the 1995 sprouts originated from flood-prostrated 1993 seedlings. In 1995 and 1993, seedlings were an order of magnitude more abundant than vegetative sprouts.

Discussion and Management Implications

Salt cedar was subdominant to Fremont cottonwood and Goodding willow in mature forest stands at the 3 rivers included in this study. To maintain or relegate salt cedar to a subdominant role, stream flows and floodplain lands need to be managed to produce ecological conditions that favor native species. This study identified several factors that influence establishment rates of salt cedar vs. native tree species.

Flood timing, magnitude, duration, and stage decline rate.—The large magnitude and long duration of the 1993 and 1995 winter floods created extensive fluvial surfaces available for colonization by woody pioneer plant species that do not tolerate competitive herbaceous cover. The long, slow decline in the river stage (flow rates did not decline to base levels until several months after the flood peaks) allowed germination of woody species with a variety of temporal regeneration niches. Extensive scour prevented herbaceous species from rapidly colonizing the moist sediments that were exposed throughout the summer, and thus germination sites were available for spring-germinating native trees (Fremont cottonwood and Goodding willow) as well as for salt cedar, a species with biseasonal seed dispersal peaks in June–July and August–September (Horton 1957, 1977, Warren and Turner 1975).

Stream flows on regulated rivers are being naturalized in several ways to facilitate establishment of Fremont cottonwood and other native species (Stanford et al. 1996, Poff et al. 1997). The same could be done to reduce establishment of salt cedar. Scouring flows should be released during early spring in potential recruitment years for cottonwoods and willows. The flood flows need to be of sufficiently high magnitude and duration to rework sediments and create bare surfaces lying within about 1 m of the "base-flow" alluvial groundwater table (Stromberg et al. 1991, 1993). Flows should peak prior to Fremont cottonwood and Goodding willow spring seed dispersal periods (from about February to April, depending on elevation). River stage should decline during the short (month long) periods of cottonwood and

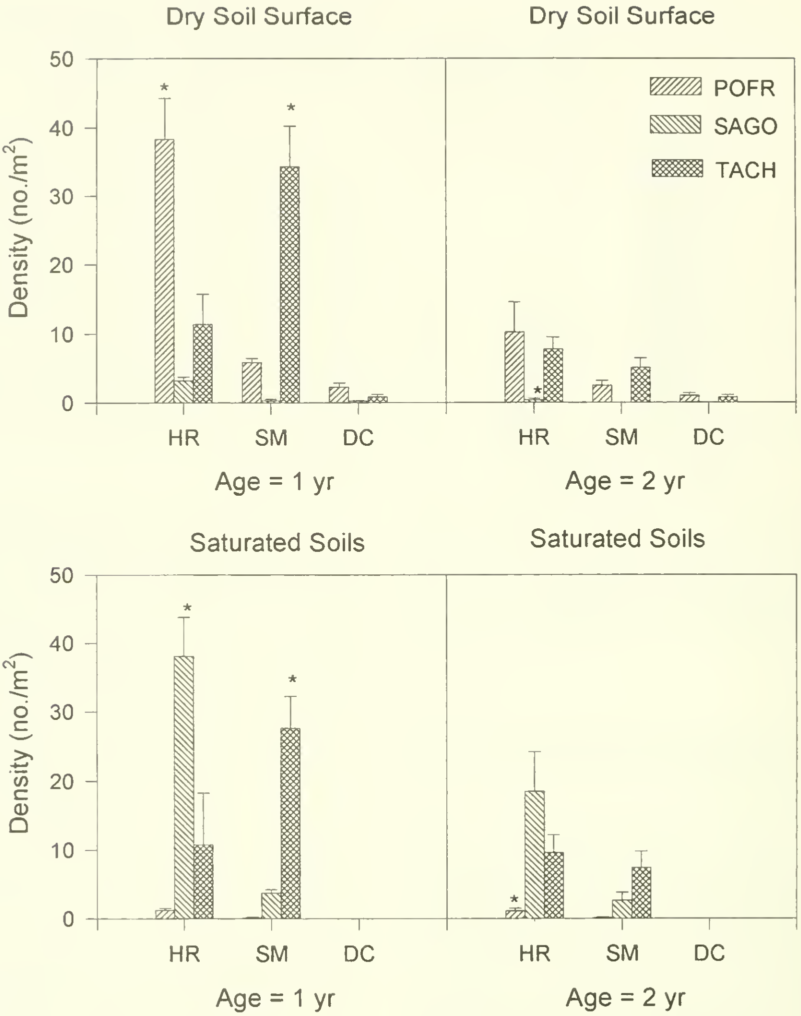

Fig. 4. Stem density of 1993 cohorts of *Populus fremontii* (POFR), *Salix gooddingii* (SAGO), and *Tamarix chinensis* (TACH), in dry surface and saturated soil zones, after 1 and 2 growing seasons (HR = Hassayampa River, SM = Santa Maria River, DC= Date Creek). Values shown are means and standard error bars. Asterisk indicates that a species had significantly different density from the other species at $P < 0.05$.

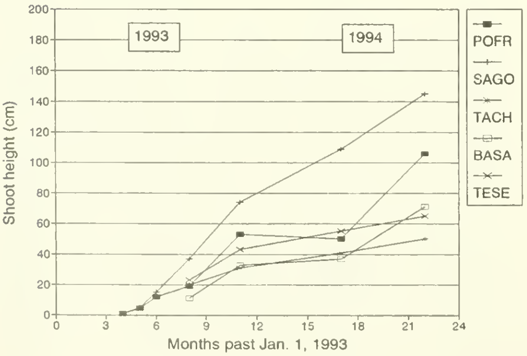

Fig. 5. Shoot heights of woody seedlings established after the 1993 flood (POFR = *Populus fremontii*, SAGO = *Salix gooddingii*, TACH = *Tamarix chinensis*, BASA = *Baccharis salicifolia*, TESE = *Tessaria sericea*).

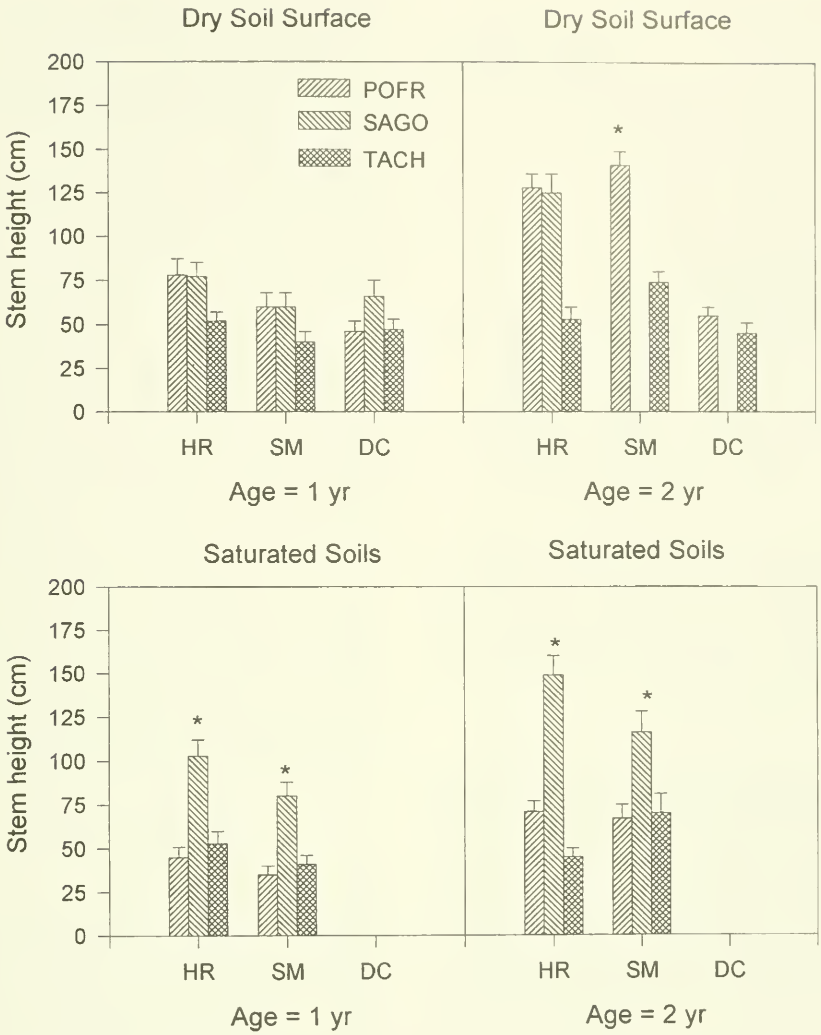

Fig. 6. Stem height of 1993 cohorts of *Populus fremontii* (POFR), *Salix gooddingii* (SAGO), and *Tamarix chinensis* (TACH), in dry surface and saturated soil zones, after 1 and 2 growing seasons (HR = Hassayampa River, SM = Santa Maria River, DC= Date Creek). Values shown are means and standard error bars. Asterisk indicates that a species had significantly different stem height from the other species at $P < 0.05$.

willow seed viability to expose moist germination sites (Mahoney and Rood 1993, Braatne et al. 1997). The rate of stage decline (and of alluvial groundwater decline) during early seedling growth should not exceed rates of root growth of Fremont cottonwood and Goodding willow seedlings. These rates are about 1–3 cm per day and vary with soil texture (Mahoney and Rood 1992, Segelquist et al. 1993). To reduce salt cedar establishment, river stage should stabilize prior to the onset of salt cedar germination in late spring. This also could reduce germination rates for summer-germinating native pioneer species such as seep willow; however, if initial flood scour is not too great, this species will rapidly regenerate asexually (Stromberg et al. 1991).

Floods that occur after seed germination also may influence relative abundance of salt cedar vs. cottonwoods and willows. In this study the 1993 seedling cohorts of Fremont cottonwood, Goodding willow, and salt cedar all had high mortality from the 1995 flood, and survivorship did not differ significantly between the 3 species. However, some studies suggest that salt cedar may be less tolerant of the scouring effects

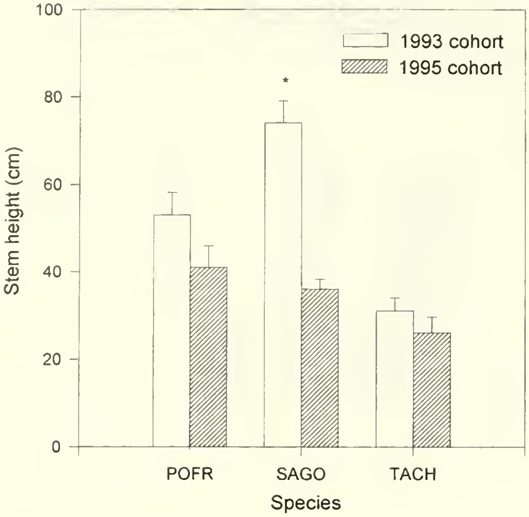

Fig. 7. Stem height of 1993 and 1995 cohorts of *Populus fremontii* (POFR), *Salix gooddingii* (SAGO), and *Tamarix chinensis* (TACH) after 1 growing season at the Hassayampa River Preserve. Values shown are means and standard error bars. Asterisk indicates signficant difference ($P < 0.05$) between cohorts.

of floods, but more tolerant of prolonged inundation, than cottonwood and willow trees (Warren and Turner 1975, Irvine and West 1979, Everitt 1980, Stevens and Waring 1985). Salt cedar seedlings may have low survivorship of floods because of their distribution in the floodplain. Because most salt cedar seeds germinate later than Fremont cottonwood and Goodding willow seeds, salt cedar seedlings sometimes are more abundant on sites close to the channel where risks of mortality from subsequent floods are high (Stromberg et al. 1991). Also, there may be physiological differences between species in tolerance for flood scour or burial by sediments. For example, low rates of shoot growth may increase the probability of complete burial of salt cedar seedlings. Existence of differential survivorship thresholds for factors such as shear stress and sediment deposition should be experimentally tested. If there are differences, release of occasional large, scouring floods in alluvial, perennial rivers in the Southwest may be a management strategy to increase the mortality of salt cedar seedlings and saplings relative to that of native pioneer tree species.

SOIL MOISTURE.—Differences in tree seedling shoot height between soil moisture zones in this study were most likely a result of differential responses to soil moisture and soil aeration. Goodding willow shoot height was greatest in conditions of saturated soils or standing water, whereas Fremont cottonwood shoot height was greatest in areas with dry surface soils but shallow water tables. Salt cedar were equally short in both zones. Comparison between years suggests that salt cedar is as tall as the native tree species under conditions of reduced water availability. Yearlings of all 3 tree species were somewhat shorter in 1995 than in 1993 (most likely due to lower river stage and deeper water tables); however, the difference between years was greater for native trees. Other studies demonstrate that salt cedar is more drought tolerant than native cottonwoods and willows and thus may have a competitive advantage on drier floodplains with deeper groundwater levels (Stevens 1987, Busch and Smith 1995). There is a need for additional controlled studies of seedling growth (Siscoe 1993, Shafroth et al. 1995) to quantify soil moisture ranges over which native species have a competitive edge. Once such ranges are described, activities that reduce floodplain water availability (such as surface water diversion and groundwater pumping) could be managed to produce soil moisture levels and groundwater depths that favor growth and survivorship of native species during establishment periods.

GRAZING.—Although this study was not explicitly designed to determine effects of livestock on riparian tree seedlings, there were differences in cattle browsing between sites which resulted in significant differences in seedling heights. At the 2 (legally) ungrazed river sites, Fremont cottonwood had a large height advantage over salt cedar in certain areas of the floodplain (i.e., dry surface soil zone). At Date Creek, which is grazed/browsed by cattle from November to March, selective browsing on Fremont cottonwood seedlings caused them to lose their height advantage over salt cedar. Between-species differences in seedling shoot height ultimately may determine the composition of the stand dominant, given that shorter plants may have greater mortality due to light limitation. All 3 species, including salt cedar, appear to be shade intolerant. Additionally, reduction in shoot height may reduce a seedling's ability to survive deposition of sediment during flood events. To favor native tree species on cattle-grazed rivers, recruitment zones should be protected year-round from livestock during at least 2 growing seasons to allow seedlings to grow above browse height.

HERBACEOUS PLANT COMPETITION.—In localized areas of the Hassayampa River floodplain, the exotic herbaceous species yellow and white sweet clover preempted establishment of salt cedar by germinating in spring and rapidly covering the ground surface prior to salt cedar germination. Fremont cottonwood seeds, in contrast, germinated prior to sweet clover. Fremont cottonwood seedlings were overtopped by sweet clover during early summer, but they were exposed to full sunlight after the midsummer death of sweet clover and had high survivorship. This suggests a possible management strategy for salt cedar, at least within small areas. If native annual species were identified that germinated after (or simultaneously with) native trees but prior to salt cedar, it might be feasible to disperse seeds of the annual herb into the floodplain at an appropriate time after large floods. However, care should be taken to insure that such an effort would reduce abundance only of salt cedar and not of "desirable" summer-germinating species such as seep willow.

ACKNOWLEDGMENTS

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ZOOGEOGRAPHIC AFFINITIES OF THE STONEFLIES (PLECOPTERA) OF THE RAFT RIVER MOUNTAINS, UTAH

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ABSTRACT.—We examined faunal affinities of the Raft River Mountains using stoneflies (Plecoptera) as indicators. This island-like mountain range is isolated from other major mountain ranges in the Intermountain West by low-elevation, arid regions. Thirty-seven species were recorded from collections made from 19 sites in the Raft River Mountains. Cluster analysis demonstrated the Raft River Mountain stonefly assemblage to be most similar to faunas of the Sawtooth and Wasatch mountains, and quite different from that of the Sierra Nevada. An analysis of the distribution patterns of each species, on a family-by-family basis, showed that the Raft River Mountains fauna consists mostly of species widespread in western North America. Most families were represented by at least 1 species whose distribution supports faunal affinities with regions to the north and west. Logistic regression of 6 long-distance dispersal factors against stonefly presence-absence data did not support long-distance dispersal as a viable means of colonization for the Raft River Mountains. This suggests that stonefly distribution patterns may be attributed to expansion and subsequent vicariance of suitable stonefly habitats during Pleistocene climatic oscillations.

Key words: Plecoptera, stoneflies, zoogeography, affinity, Pleistocene, Great Basin, Raft River Mountains, Utah.

Biogeographic properties of island-like mountain ranges in the Intermountain West have been a topic of much research (MacArthur and Wilson 1963, Brown 1971, Johnson 1975, Behle 1978, Harper et al. 1978, Wells 1983). These mountain islands are appealing as opportunities to study the distribution, diversity, and evolution of organisms inhabiting them. The Raft River Mountains in extreme northwestern Utah are such a mountain range, and various studies have recognized that they are distinct from nearby regions (Durrant 1952, Behle 1958, McMahon and Wiebolt 1978).

McMahon and Wiebolt (1978) used a classification system developed by Holdridge (1947) and Holdridge et al. (1971) to divide Utah into "life zones" based on mean annual temperature, mean annual precipitation, and potential evapotranspiration. According to their classification, the Raft River Mountains are an ecologically isolated island of subtropical, montane, moist forest surrounded by regions of montane steppe and desert (McMahon and Wiebolt 1978).

Durrant (1952) concluded that the Raft River Mountains have mammal faunal affinities with the Columbia Plateau. His conclusions were based on 2 unique mammal species, *Tamias amoenus* Allen (yellow pine chipmunk) and *Citellus beldingi* Hall (Belding ground squirrel), both found in the Raft River Mountains but nowhere else in Utah. In addition, the broader distributions of these species extend north and west into regions associated with the Columbia Plateau (Durrant 1952).

The damselfly, *Calopteryx aequabilis* Say, and rugose stag beetle, *Sinodendron rugosum* Mann, are insects in the Raft River Mountains with interesting faunal affinities. *Calopteryx aequabilis* is known to occur throughout most of Canada, the north central and northeastern United States, and in isolated pockets in the western United States, including the Columbia River drainage (Provonsha 1975). *Sinodendron rugosum* has an overall distribution outside Utah that includes Idaho, Washington, Oregon, California, and British Columbia (Essig 1929, Hatch 1971).

Behle (1958) lists 172 bird species and subspecies from the Raft River Mountains and concludes that the bird assemblage in the Raft River Mountains more closely resembles that of the Great Basin than the nearby Wasatch Mountains.

The most desirable organisms to use when studying patterns of faunal affinities are those

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restricted to definable habitats (Sargent et al. 1991). Stoneflies (Plecoptera) are such a model group (Nelson 1994). Many stonefly species have limited ranges, and distinctive differences occur between the stonefly faunas of the Rocky Mountains, the Coast and Cascade mountains, and the Sierra Nevada (Jewett 1959).

Stoneflies depend on a water connection, with very specific habitat requirements (Surdick and Gaufin 1978, Baumann 1979), to expand their distribution. They are greatly influenced by water temperatures (Baumann 1979), pollution levels (Surdick and Gaufin 1978), and dissolved oxygen concentrations (Gaufin et al. 1966). Rocky streambeds or rocky lakeshores often are required for nymphs to complete their development (Gaufin et al. 1966, Hynes 1976), and the riparian environment is important for adult stoneflies to survive and successfully reproduce once they emerge from the final nymphal instar.

Adult stoneflies normally fly only short distances (Marden and Kramer 1994), and many are short-winged, which further reduces flying ability. Additionally, phenology of adult emergence may have an effect on the distribution of many species. For example, species in the family Capniidae emerge only during winter through breaks in the ice (Frison 1929). Species in this family are generally more limited in their distributions than those of other families (Nebeker and Gaufin 1967) that emerge during seasons when habitats and temperatures are more conducive to dispersal.

In this study we examine species composition, faunal affinities, and long-distance dispersal potential of stoneflies in the Raft River Mountains. We compare species composition with that from 3 other regional mountain ranges to determine overall similarity between their stonefly faunas and possible modes of colonization. The Sawtooth Mountains in central Idaho, Wasatch Mountains in northern Utah, and Sierra Nevada in California are regions with which the Raft River Mountains stonefly fauna may have affinities.

STUDY AREA

The Raft River Mountains, near the borders of Utah, Idaho, and Nevada in extreme northwestern Utah, resemble a gently sloping plateau that rises from surrounding arid basins to an elevation of 2900 m. The range has an area of approximately 990 km^2 and lies in an east–west orientation as part of the northern edge of the Great Basin.

Considerable differences in vegetation and precipitation exist between the north and south slopes of these mountains due to their east–west orientation (Behle 1958). Northern slope streams are unique in Utah since they flow into the Snake River drainage system. Southern drainages that once flowed into Pluvial Lake Bonneville (Stokes 1987) now drain into the Bonneville Basin.

The insular nature of this mountain range makes it excellent for testing biogeographical hypotheses. Immediately surrounding the Raft River Mountains are arid lowlands (Great Basin, Bonneville Basin, and Snake River Plain), which effectively isolate them from other mountain ranges in the region (Fig. 1). The Bonneville Basin currently isolates the Raft River Mountains from the Wasatch Mountains to the southeast, the Snake River Plain is a barrier for stonefly dispersal from the Sawtooth Mountains in central Idaho (Nebeker and Gaufin 1967), and the Great Basin isolates the Raft River Mountains from the Sierra Nevada (Nebeker and Gaufin 1967, Brown 1971, Johnson 1975). For purposes of this study, we consider these 3 mountain ranges as hypothesized source pools for stonefly dispersal to the Raft River Mountains.

METHODS

We visited most major drainages in the Raft River Mountains at least once during each season for 2 yr. We collected data during 1994–95 and also included previous collection records from 1977 to 1980.

Stonefly nymphs were collected using an aquatic kick net. Adults were collected with a beating sheet from riparian vegetation and with ultraviolet light traps near streams at night. Exuviae were also collected.

Nymphal and adult stoneflies were preserved in 70% ethyl alcohol and identified to the lowest possible taxon using current identification keys (Baumann et al. 1977, Nelson and Baumann 1987, 1989, Stewart and Stark 1988, and Stanger and Baumann 1993).

Species lists from the Sawtooth Mountains, Wasatch Mountains, and Sierra Nevada were compiled directly from the literature (Jewett

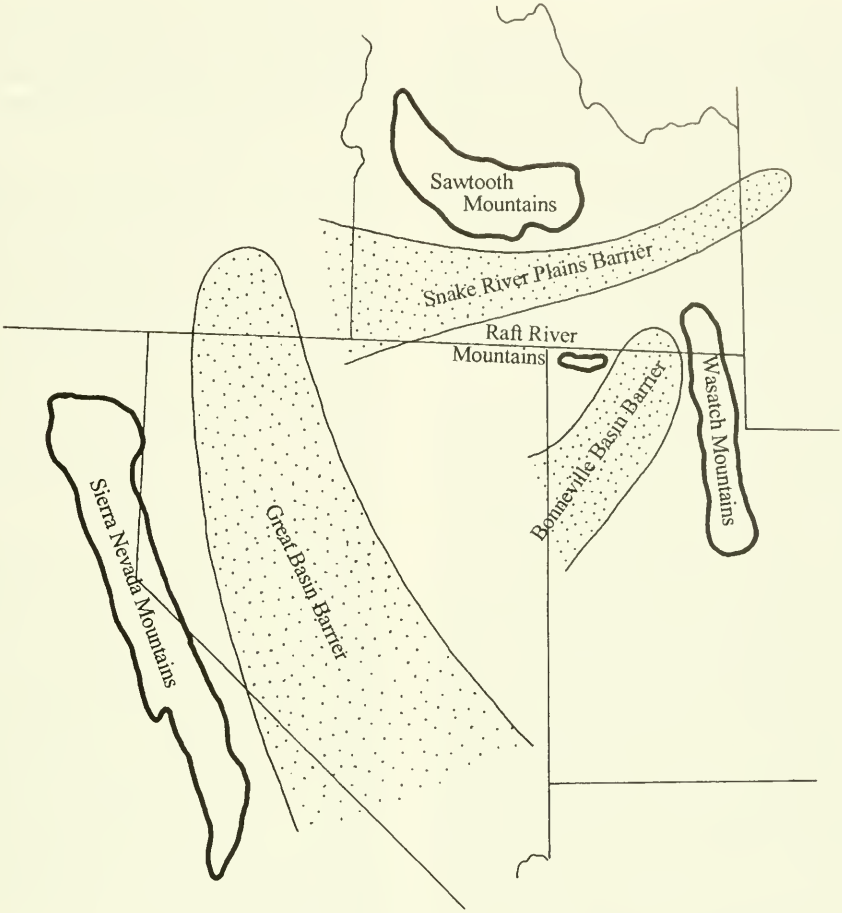

Fig. 1. Mountain ranges considered in this study and intervening barriers for stonefly dispersal.

1960, Nebeker and Gaufin 1965, Gaufin et al. 1966, Logan and Smith 1966, Nebeker and Gaufin 1966, Sheldon and Jewett 1967, Baumann and Gaufin 1969, Newell and Minshall 1976, Baumann et al. 1977, Nelson and Baumann 1987, 1989, Kondratieff and Baumann 1988, Stanger and Baumann 1993, and Stark and Nelson 1994). We annotated counties with any portion of these mountain ranges within their boundaries and assumed that records from these counties indicated the presence of a species in that particular mountain range.

We investigated faunal affinities of each species collected in the Raft River Mountains by examining its distribution in North America. Each species was classified according to the region of faunal affinity it supports.

Similarities between stonefly species composition of the Raft River Mountains and the 3 hypothesized source pool mountain ranges were determined with cluster analysis using NTSYS-pc 1.70 (Rohlf 1992). Stonefly presence-absence data were entered into a matrix from which a distance matrix was constructed using Jaccard's coefficient. The distance matrix, which quantifies the similarity between a pair of areas as a decimal value, was SAHN (sequential, agglomerative, hierarchical, nested) clustered using UPGMA (unweighted pairs-group method with arithmetic averaging). Single-link and complete-link methods were also employed. All clustering methods resulted in dendrograms that demonstrate similarities of faunal composition between mountain ranges.

Since SAHN will produce clusters whether or not natural groups are present in the data (Rohlf 1992), a cophenetic value matrix was computed from the dendrogram matrix to analyze goodness of fit between the cluster dendrogram matrix and distance matrix. The cophenetic matrix was compared element by element with the original distance matrix according to a test developed by Mantel (1967). This comparison produces a product-moment correlation, *r*, which measures the degree of relationship between the distance matrix and dendrogram matrix. Values >0.90 indicate that the tree accurately represents natural groupings present in the data. Values <0.70 indicate that natural groups may not be present (Rohlf 1992).

Dispersal abilities were quantified for all stonefly species recorded from the hypothesized source pool mountain ranges. Scores for dispersal ability were based on published data for 6 factors that influence stonefly distribution and long-distance dispersal (Logan et al. 1966, Nebeker et al. 1966, Baumann et al. 1977, Surdick and Gaufin 1978, Baumann 1979, Nelson and Baumann 1987, 1989, Kondratieff and Baumann 1988, Stanger and Baumann 1993): season of emergence, length of emergence, distribution within the source mountain range, relative distance from the Raft River Mountains, environmental tolerance, and wing length (Table 1). If colonization of the Raft River Mountains by stoneflies occurred via random, long-distance dispersal, one would expect the Raft River Mountains fauna to be composed of species with high quantified dispersal ability (Coleman et al. 1982).

We used logistic regression analysis (P = 0.05) to test for correlation between high scores for these 6 factors and stonefly presence-absence data in the Raft River Mountains. Significant correlation would provide evidence for long-distance dispersal as a mode of colonization for those stonefly species found in these mountains.

WING LENGTH.—Because macropterous (long-winged) stoneflies are better fliers than brachypterous (short-winged), micropterous (minutely-winged), or apterous (without wings; Marden and Kramer 1994), they were assumed to be better adapted for long-distance dispersal. Both sexes were examined for wing morphology and scored according to wing length. Apterous or micropterous species of either sex were given a score of 1. Species with brachypterous members of either sex were scored 2, and species where both sexes were macropterous received a score of 3.

ECOLOGICAL TOLERANCE.—Species that survive in a broader range of ecological conditions were assumed to be better adapted for long-distance dispersal because a broad tolerance allows a species to survive in a greater number of post-dispersal environments. Baumann (1979) identifies 3 stonefly environments, cold lotic, warm lotic, and cold lentic, and calls them "ecological groupings." Species that are limited to only 1 of these ecological groupings received a score of 1, species in 2 of these groupings were scored 2, and those species capable of living in all 3 ecological groupings were given a score of 3.

SEASON OF EMERGENCE.—Dispersal is more probable during warmer seasons (Nebeker and Gaufin 1967). Fall- or winter-emerging species received a score of 1, spring-emerging species

TABLE 1. Characteristics important for stonefly long-distance dispersal. Each characteristic is divided into 3 categories and scored according to assumed influence on long-distance dispersal to the Raft River Mountains (1 = low, 2 = medium, 3 = high).

	Category and score		
Characteristic	1	2	3
Season of emergence	Fall or winter	Spring	Summer
Length of emergence	1–3 months	4–5 months	6–12 months
Ecological tolerance	1 grouping	2 groupings	3 groupings
Wing length	apterous or micropterous	brachypterous	macropterous
Relative distance from Raft River Mountains	farthest 1/3	middle 1/3	closest 1/3
Distribution within source mountain range	1 of 3 regions	2 adjacent regions	2 nonadjacent or 3 regions

were scored 2, and summer-emerging species were scored 3. September through February was considered fall and winter; spring months were considered April and May; and June through August was considered summer.

LENGTH OF EMERGENCE.—We assumed dispersal to be more probable for species whose adults are present for longer periods of time. By using emergence and collection records, we determined how many months during the year adults are present for each source pool mountain range. Species whose adults were present up to 3 months were given a score of 1, presence during 4–5 months of the year was scored 2, and species with adults present >5 months were scored 3.

DISTRIBUTION WITHIN HYPOTHESIZED SOURCE MOUNTAIN RANGES.—Long-distance dispersal was assumed to be more probable for species with widespread distributions in the hypothesized source mountain ranges. To assess how widespread each species was within a source pool mountain range (Sierra Nevada, Sawtooth, Wasatch), we subdivided each mountain range along its length into 3 equally sized regions. If a species was recorded from only 1 of these regions, we scored it as 1. If a species' distribution covered 2 adjacent regions, it was scored 2. Presence in all 3 regions was scored 3. If a species was present in the regions at opposite ends of the mountain range, we assumed it also was present in the middle and scored it 3.

RELATIVE DISTANCE FROM THE RAFT RIVER MOUNTAINS.—Dispersal is more likely between areas nearer to each other (MacArthur and Wilson 1963). We measured straight-line distances from the Raft River Mountains to the single nearest and most distant counties. Nearest was Cache County in the Wasatch Mountains and farthest was Kern County in the Sierra Nevada. Once the nearest and most distant counties were located, we calculated the difference in distance between them and divided it into thirds. Species whose nearest literature record was from a county in the most distant third were scored 1. If the closest record was from a county in the middle third, it was scored 2. Species from the nearest third were scored 3.

RESULTS

We collected 37 species in 25 genera and 8 families from the Raft River Mountains. They are listed in Table 2 by collection site and presence in each source mountain range. Of these 37 species, 5 are unique records for Utah and have distributions extending outside the state to the northwest: *Malenka tina* (Ricker), *Taeniopteryx nivalis* (Fitch), *Capnia petila* Jewett, *Capnura intermontana* Nelson and Baumann, and *Doroneuria* sp. In addition, a potentially undescribed species in the genus *Kogotus* was collected in several of the Raft River Mountain drainages.

Literature records contain 82 species in 41 genera and 9 families for the Sierra Nevada (Jewett 1960, Nebeker and Gaufin 1965, Sheldon and Jewett 1967, Nelson and Baumann 1987, 1989, Kondratieff and Baumann 1988, Stanger and Baumann 1993, and Stark and Nelson 1994). There are 62 species in 32 genera and 8 families in the Wasatch Mountains (Nebeker and Gaufin 1965, Gaufin et al. 1966, Baumann and Gaufin 1969, Baumann et al. 1977, Nelson and Baumann 1987, 1989, Kondratieff and Baumann 1988, and Stanger and Baumann 1993). The Sawtooth Mountains have 70 species in 33 genera and 9 families (Nebeker and Gaufin 1965, 1966, Logan and Smith 1966, Baumann et al. 1977, Nelson and Baumann 1987, 1989, Kondratieff and Baumann 1988, Stanger and Baumann 1993, and Stark and Nelson 1994).

UPGMA clustering suggested that stonefly species composition of the Raft River Mountains was most similar to the Sawtooth Mountains. Species composition is also similar to the Wasatch Mountains and different from the Sierra Nevada (Fig. 2). A matrix correlation of $r = 0.94$ demonstrated a good fit between the dendrogram data and taxonomic distance matrix. These data support previous findings by Nelson (1994), Harper et al. (1978), and Wells (1983).

Single and complete-link methods produced the same tree topology as UPGMA, and similar cluster and matrix correlation values were obtained. Single-link clustering produced similarity values of 0.431, 0.407, and 0.272 with a matrix correlation $r = 0.94$. Complete-link cluster values were 0.431, 0.375, and 0.272 with a matrix correlation value $r = 0.94$.

Clear Creek yielded the highest number of species. However, this is probably a result of the number of different times the site was sampled. The number of species per site and the number of times a site was sampled had a

TABLE 2. Stonefly species records and collection sites in the Raft River Mountains and records for these species in the Sawtooth Mountains, Sierra Nevada, or Wasatch Mountains.

	Collection sites by number																		
	Raft River – North Slope									Raft River – South Slope							Source ranges		
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Pteronarcys princeps	x	x	x	x		x								x	x	x		x	x
Pteronarcella badia	x	x	x	x		x								x	x	x	x		x
Doddsia occidentalis	x	x	x	x											x		x	x	x
Taenionema pallidum	x	x	x	x											x		x	x	x
Taeniopteryx nivalis							x										x	x	
Podmosta decepta	x	x		x											x		x		
Podmosta delicatula		x															x	x	x
Prostoia besametsa	x	x	x	x			x							x	x		x	x	x
Zapada cinctipes	x	x	x	x						x	x			x	x	x	x	x	x
Zapada haysi			x											x	x		x	x	x
Malenka californica	x	x	x	x													x	x	x
Malenka tina	x	x							x			x					x		
Paraleuctra vershina	x	x		x										x	x	x	x	x	x
Capnia gracilaria	x	x	x	x										x	x	x	x		x
Capnia petila															x		x		
Capnia vernalis							x	x									x		x
Capnura intermontana							x										x		
Eucapnopsis brevicauda				x										x			x	x	x
Utacapnia lemoniana	x	x		x						x							x		x
Doroneuria sp.	x	x															x	x	
Hesperoperla pacifica	x	x	x	x						x	x			x	x	x	x	x	x
Diura knowltoni	x	x	x	x										x	x		x	x	x
Isoperla fulva							x										x	x	x
Isoperla pinta							x										x	x	x
Isoperla quinquepunctata			x				x			x				x			x	x	x
Isoperla sobria				x											x			x	x
Kogotus sp. A	x	x	x	x									x		x				
Megarcys signata	x	x		x										x	x	x	x		x
Skwala americana							x									x	x	x	x
Suwallia lineosa	x			x								x	x		x		x		x
Suwallia pallidula	x	x															x	x	x
Sweltsa borealis				x											x		x	x	x
Sweltsa coloradensis	x	x	x	x	x							x		x	x	x	x		x
Sweltsa lamba	x		x	x								x		x	x		x		x
Triznaka pintada			x			x						x					x	x	x
Triznaka signata	x	x	x	x								x					x		x
Utaperla sopladora	x	x		x											x	x	x	x	x
Species richness	23	22	17	23	1	3	8	1	1	4	2	6	2	14	21	10	34	22	29
Collection visits	13	13	11	12	1	1	11	1	2	8	1	4	1	5	9	6			

1. Clear Creek Campground
2. Clear Creek Lower Bridge
3. One Mile Creek
4. George Creek
5. Wildcat Creek
6. Johnson Creek
7. Raft River, Upper Narrows
8. Raft River, Lower (Idaho)
9. Junction Creek
10. Dove Creek
11. Twin Creek
12. Big Hollow Creek
13. Left Fork Pine Creek
14. Rock Creek
15. Fisher Creek
16. Dunn Creek
17. Sawtooth Mountains
18. Sierra Nevada
19. Wasatch Mountains

correlation coefficient of 0.87. The Upper Narrows of the Raft River displayed the greatest amount of local endemism. This is the only site in the Raft River Mountains where *Taeniopteryx nivalis* (Fitch), *Capnia vernalis* Newport, *Capnura intermontana* Nelson and Baumann, *Isoperla fulva* Claassen, and *Isoperla pinta* Frison occur. *Podmosta delicatula* (Claassen), *Doroneuria* sp., and *Suwallia pallidula* (Banks) were collected only from Clear Creek, and *Capnia petila* was found only in Fisher Creek.

A distribution analysis of the 37 species based on their occurrence in either northern or southern drainages showed that 36 of 37

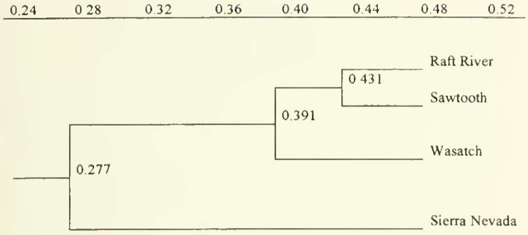

Fig. 2. UPGMA dendrogram of similarity between the Raft River Mountains, Sawtooth Mountains, Sierra Nevada, and Wasatch Mountains stonefly species assemblages.

species (97%) were collected in northern drainages, *Capnia petila* being the exception. Only 28 of 37 (76%) species were collected in southern drainages. Of the 9 species not collected from southern drainages, 5 from the Upper Narrows of the Raft River and 3 from Clear Creek (both northern drainages) were not found elsewhere in the study area. These 2 sites alone accounted for 32 of 37 (84%) total species collected in the Raft River Mountains. Differences in northern versus southern drainage diversity are almost completely explained by the uniqueness of these 2 sites.

Logistic regression analysis of the 6 factors affecting stonefly long-distance dispersal found that distance was the only factor significantly correlated with stonefly presence-absence data in the Raft River Mountains. Every species collected in the Raft River Mountains was also found in the closest distance category. Those species in the middle or farthest distances were present in the Raft River Mountains only if they were also present in the nearest distance. An additional analysis of the remaining 5 factors for only those species within the nearest distance category also demonstrated that none are significantly correlated with stonefly presence-absence in the Raft River Mountains. A long-distance dispersal model does not explain presence-absence data for the Raft River Mountains.

DISCUSSION

Faunal Affinities

Distributions of each species in the Raft River Mountains, on a family-by-family basis, showed some interesting patterns of faunal affinity not revealed by analyses of overall similarity.

PTERONARCYIDAE.—*Pteronarcys princeps* Banks is abundant throughout the Pacific Northwest and California but rare in the Rocky Mountains (Jewett 1959, Baumann et al. 1977). Its presence in the study area supports a faunal relationship with regions to the northwest. *Pteronarcella badia* (Hagen) is common in the Rocky Mountains, extends into the Pacific Northwest (Baumann et al. 1977), but is absent in the Sierra Nevada.

Pteronarcys californica Newport was absent from the Raft River Mountains, even though it is commonly found throughout the West (Baumann et al. 1977). Its absence is due probably to lack of high-quality, large rivers in the study area.

TAENIOPTERYGIDAE.—*Taeniopteryx nivalis*, commonly found in eastern North America, is rare in the West, being limited to western Canada and the Pacific Northwest (Ricker 1964, Kondratieff and Baumann 1988). Ricker (1964) attributed this distribution to a postglacial or interglacial dispersal across Canada and down the Rocky Mountains with subsequent extinction in central Canada. *Taeniopteryx nivalis* reaches the southernmost part of its range in the Raft River Mountains where its presence indicates a faunal relationship between these mountains and areas to the northwest.

Doddsia occidentalis (Banks) and *Taenionema pallidum* (Banks) were both found in the Raft River Mountains and are widely distributed in western North America (Baumann et al. 1977). They are not useful species for determining faunal affinities with any particular region.

Taenionema pacificum (Banks) is widespread in western North America from Alaska to New Mexico (Stanger and Baumann 1993), but the absence of sufficiently large rivers in the Raft River Mountains may explain why it was not collected in this study.

NEMOURIDAE.—*Malenka californica* (Claassen), *Podmosta delicatula*, *Podmosta decepta* (Frison), *Prostoia besametsa* (Ricker), *Zapada cinctipes* (Banks), and *Zapada haysi* (Ricker) are all widely distributed in western North America (Baumann et al. 1977) and occur in the Raft River Mountains, giving no clear indication of faunal affinities.

The presence of *Malenka tina* supports faunal relationships between the Raft River Mountains and regions to the northwest (Jewett 1959).

CAPNIIDAE.—Species in this family typically have limited distributions (Nebeker and Gaufin 1967). Only 1 species, *Eucapnopsis brevicauda* Claassen, was collected in all 3 hypothesized regions of faunal affinity.

Capnia gracilaria Claassen, *Capnia vernalis*, and *Utacapnia lemoniana* (Nebeker and Gaufin) were shared by the Raft River, Sawtooth, and Wasatch mountains. *Capnia gracilaria* is also found in the Pacific Northwest but does not support faunal affinities with that region since its overall distribution is much more widespread.

Capnia petila and *Capnura intermontana* were shared only by the Sawtooth Mountains. The presence of *C. petila* in the study area represents the southernmost collection of this species in western North America. It supports a faunal relationship with northern regions of the Rocky Mountains but not with the Pacific Northwest. *Capnura intermontana* is limited to drainages in the northern Great Basin and tributaries of the Snake River (Nelson and Baumann 1989, Nelson 1994). It indicates faunal relationships between the Raft River Mountains and regions to the north and west.

PERLODIDAE.—Eight species from this family were collected in the Raft River Mountains. Seven of these, *Diura knowltoni* (Frison), *Isoperla fulva* Claassen, *Isoperla pinta* Frison, *Isoperla quinquepunctata* (Banks), *Isoperla sobria* (Hagen), *Megarcys signata* (Hagen), and *Skwala americana* (Frison), are relatively widespread in western North America (Baumann et al. 1977).

An interesting species, *Kogotus* sp. A, with brachypterous wings was collected in the Raft River Mountains and further west in the Jarbridge Mountains of north central Nevada. Two other species of *Kogotus* occur in western North America: *Kogotus nonus* (Needham and Claassen) in the Coast and Cascade ranges, and *Kogotus modestus* (Banks) in the Rocky Mountains (Jewett 1959). *Kogotus* sp. A in the Raft River Mountains may be a potential new species with distribution between *K. nonus* and *K. modestus*.

PERLIDAE.—Only nymphs of *Doroneuria* sp. were collected, and since identification at the species level is possible only with adult specimens, we could not positively identify this species as *D. theodora* (Needham and Claassen) or *D. baumanni* Stark and Gaufin.

Hesperoperla pacifica (Banks) has a broad distribution in western North America and does not give any indication of affinity.

CHLOROPERLIDAE.—*Suwallia pallidula* (Banks), *Sweltsa borealis* (Banks), and *Triznaka pintada* (Ricker) were shared by all mountain ranges considered in this study. *Suwallia lineosa* (Banks), *Sweltsa coloradensis* (Banks), *Sweltsa lamba* (Needham and Claassen), and *Triznaka signata* (Banks) were shared between the Raft River, Sawtooth, and Wasatch mountains only. Since these species all have such widespread distributions, they indicate little about faunal affinities with any single region.

Utaperla sopladora is primarily a northern Rocky Mountain species, and its presence in the Raft River Mountains indicates faunal affinities with regions to the north. Extensive collecting has failed to find this species in the Wasatch Mountains (Baumann et al. 1977) or the Pacific Northwest (Jewett 1959).

PELTOPERLIDAE.—No species in this family were collected from the Raft River or Wasatch mountains, but it was represented by *Yoraperla brevis* (Banks) in the Sawtooth Mountains and *Yoraperla nigrisoma* (Banks) in the Sierra Nevada (Stark and Nelson 1994). The Pacific Northwest also has several peltoperlid species (Jewett 1959), and their absence in the Raft River Mountains implies a lack of strong faunal relationships with regions to the northwest.

In summary, faunal affinities of those species and families collected in the Raft River Mountains indicate the Plecoptera fauna is composed of 2 dominant groups (Table 3). The largest group (68% of 37 species) consists of species widely distributed in western North America. Species associated with regions north and west of the Raft River Mountains constitute the 2nd group and represent 22% of the Raft River Mountains fauna. Most families in the study are represented by at least 1 species from this 2nd group. Similarities revealed by cluster analysis are the result of repeated faunal relationships within each family and not the result of any single family influencing overall similarity patterns.

Colonization

The Raft River Mountains provide a good model of an island habitat; however, geologic history indicates they have not been completely

TABLE 3. Stonefly species found in the Raft River Mountains listed by family and region of faunal affinity each supports.

	Region of faunal affinity		
Family	Widespread	Northwestern	Other
Pteronarcyidae		*Pteronarcys princeps*	*Pteronarcella badia*
Taeniopterygidae	*Doddsia occidentalis*	*Taeniopteryx nivalis*	
	Taenionema pallidum		
Nemouridae	*Malenka californica*	*Malenka tina*	
	Podmosta delicatula		
	Podmosta decepta		
	Prostoia besametsa		
	Zapada cinctipes		
	Zapada haysi		
Leuctridae	*Paraleuctra vershina*		
Capniidae	*Eucapnopsis brevicauda*	*Capnia petila*	*Capnia vernalis*
	Capnia gracilaria	*Capnura intermontana*	*Utacapnia lemoniana*
Perlodidae	*Diura knowltoni*		*Kogotus* sp. A
	Isoperla fulva		
	Isoperla pinta		
	Isoperla quinquepunctata		
	Isoperla sobria		
	Megarcys signata		
	Skwala americana		
Perlidae	*Hesperoperla pacifica*	*Doroneuria* sp.	
Chloroperlidae	*Suwallia pallidula*	*Utaperla sopladora*	
	Suwallia lineosa		
	Sweltsa borealis		
	Sweltsa coloradensis		
	Sweltsa lamba		
	Triznaka pintada		
	Triznaka signata		

isolated from these hypothesized colonization sources in the past (Petersen et al. 1980). Climatic changes caused by Pleistocene glacial and interglacial cycles had a profound effect on biotic distributions and connectedness of habitats within the Great Basin region (Axelrod 1981, Grayson 1993). These climatic oscillations provided the mechanism for a vicariance model of stonefly colonization in the Raft River Mountains.

Pleistocene climatic changes directly affected the location of stonefly habitats in North America. Cooler climates moved south from polar regions and pushed stonefly habitats further south and into the lower elevations of the Intermountain West (Sargent et al. 1991). Increased precipitation and subsequent runoff from glaciers caused an overall expansion of pluvial environments. Stonefly habitats expanded into generalized tracks of distribution (Croizat et al. 1974). The later retreat of glaciers moved stonefly habitats northward and into higher elevations. Island-like habitats were isolated by intervening lowlands and dry lakebeds. This occurred most recently within the last 10,000 yr (Stokes 1987).

During glacial intervals corridors were opened between the Raft River and other mountain ranges to the north and west. Species in regions to the north and west were able to reach their southernmost distributions in the Raft River Mountains before vicariance isolated them. These same corridors of distribution did not exist between the Raft River Mountains and Sierra Nevada due to the presence of extremely low elevation valleys in western Nevada (Wells 1983). This explains why all species shared between the Raft River Mountains and Sierra Nevada are also present in the Rocky Mountains.

The vicariance argument is strengthened by repeated patterns of affinity for each of the stonefly families present in the Raft River Mountains. Similar patterns exist for mammals (Durrant 1952, Brown 1971) and plants (Billings 1978, Harper et al. 1978) in the Great Basin. Similarities in distribution patterns for different taxonomic groups are undoubtedly the result of a vicariant event splitting all biotas rather than multiple long-distance dispersal events. Stonefly distribution patterns in the southwestern United States (Stewart et al. 1974) and northern Mexico (Sargent et al. 1991) have also been attributed to vicariance events during the Pleistocene.

CONCLUSIONS

The stonefly fauna of the Raft River Mountains consists of 37 species in 25 genera and 8 families. Five are unique records for the state of Utah, and 1 is a potentially undescribed species in the genus *Kogotus*.

Most species collected in the Raft River Mountains are those with widespread distributions in western North America. Repeated patterns of faunal affinity for most stonefly families show strong faunal affinities with stonefly assemblages in the Rocky Mountains to the north. Of the mountain ranges examined, the Raft River Mountains stonefly fauna most closely resembles that of the Sawtooth Mountains in central Idaho.

Logistic regression analysis demonstrated that a long-distance dispersal model of stonefly colonization cannot explain patterns of presence-absence in the Raft River Mountains. Stonefly distributions in the Raft River Mountains appear to be the result of expanded stonefly distributions and subsequent vicariance caused by Pleistocene climatic oscillation.

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BROOD-REARING HABITAT USE BY RIO GRANDE WILD TURKEYS IN OREGON

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ABSTRACT.—Wild turkey (*Meleagris gallopavo*) brood-rearing sites have been described for portions of their range, but brood-rearing habitat use and characteristics of brood-rearing sites used by Rio Grande Wild Turkeys (*M. g. intermedia*) in the Pacific Northwest were unknown. We described cover types at 362 brood-rearing sites and measured habitat characteristics at 64 of these sites used by a recently established Rio Grande Wild Turkey population in southwestern Oregon during May–September 1989 and 1990. Hens with broods used 9 of 10 available cover types. Meadows, mixed hardwood/conifer woodlands, and savannas were used more often than expected (47% of observations, $P \leq 0.05$). Broods used mature mixed conifer and dense sapling/pole mixed conifer cover types less than expected and did not use brushfields. Many brood-rearing sites were characterized by a parklike appearance. Understory vegetation averaged <20 cm tall and occupied 44–52% of brood-rearing sites, whereas bare ground accounted for 35–55%. Brood-rearing sites were on southeast slopes more often than expected and north slopes less than expected ($P \leq 0.05$). We suggest that land managers maintain mixed hardwood/conifer woodland and savanna cover types adjacent to meadows on south slopes to provide brood-rearing habitat for Rio Grande Wild Turkeys in southwestern Oregon.

Key words: Rio Grande Wild Turkey, brood rearing, habitat use, site characteristics, Oregon, radio telemetry, Meleagris gallopavo intermedia.

Rio Grande Wild Turkeys are native to the south central Great Plains of North America, but translocation programs established populations in 9 western states (Wunz 1992). Variability in wild turkey movements and home ranges among geographic regions and subspecies was attributed primarily to variation in resource availability (Brown 1980). Wild turkeys frequently demonstrated a high level of adaptability by using a variety of cover types but selected specific vegetative characteristics within cover types (Holbrook et al. 1987).

Environmental factors that affect brood-rearing habitats are critical to population maintenance. Everett et al. (1980) suggested that poult survival is directly related to the suitability of brood-rearing habitat. Vegetative composition and structure in brood range influence protection from predators, poult mobility, arthropod abundance, and exposure to dew (which can induce hypothermia). Brood-rearing habitats have been described as parklike with moderate understory vegetation and nearby escape cover (Porter 1992). Habitat use by adult Rio Grande Turkeys in their native range was studied extensively (e.g., Logan 1974, Baker et al. 1980), but quantitative descriptions of brood-rearing habitats are lacking. Brood-rearing habitat use by introduced Rio Grande Wild Turkey populations received little attention or was investigated in simple systems (e.g., 2–3 cover types). Because brood-rearing habitat is important in maintaining wild turkey populations, we examined habitat use by Rio Grande Wild Turkey hens with poults in southwestern Oregon and quantified brood-rearing site characteristics.

STUDY AREA

The 675-km^2 study area is in the upper South Umpqua River Basin, Douglas County, Oregon. Elevation ranges from 310 to 1525 m, and the area is dissected by steep east–west ridges. Franklin and Dyrness (1973:130) attributed the heterogeneous association of plant cover types in this area to diverse edaphic and geologic conditions. Overstories are dominated by Douglas fir (*Pseudotsuga menziesii*) and other conifers or Oregon white oak (*Quercus garryana*) and Pacific madrone (*Arbutus menziesii*). Deciduous midstory tree species include Oregon ash (*Fraxinus latifolia*) and big-leaf maple (*Acer macrophyllum*). Common shrubs include poison oak (*Rhus diversiloba*), Oregon grape (*Berberis* spp.), ceanothus (*Ceanothus* spp.), and manzanita (*Arctostaphylos* spp.). Plant nomenclature follows Hitchcock and Cronquist (1973). The Oregon Department of Fish and Wildlife (ODFW) released 58 Rio Grande Wild Turkeys from Texas and Kansas on the study area in 1982 and 1983 (R.R. Denney, ODFW, unpublished data).

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METHODS

Capture and Radio Telemetry

We used rocket nets to capture turkeys during January 1989 and from December 1989 through February 1990. Hen age (yearling or adult) was assigned from characteristics of primary feathers (Larson and Taber 1980), and we equipped hens with 90- to 110-g radio transmitters attached with modified backpack harnesses (Kenward 1987:103). Transmitters were equipped with motion-sensitive switches; expected transmitter life ranged from 1 to 3 yr.

During 2 trapping seasons we captured 181 wild turkeys. In 1988–89 we equipped 26 adult and 19 yearling hens with transmitters. Fifteen adults and 15 yearlings (considered adults during the 2nd yr) survived to 1990. In the 1989–90 trapping season, we equipped 10 additional adults and 21 yearlings with transmitters, bringing the total sample to 36 adult and 40 yearling hens. All radio-marked hens survived ≥ 2 wk after release. We monitored 46 hens for 1 nesting season and 17 for 2 seasons. We did not monitor 26 hens during nesting seasons because of deaths or transmitter failures (19 adult, 7 yearling). Therefore, the approximate maximum potential sample was 80 broods during the 2-yr period. This was an approximation because some hens renested after brood loss, producing 2 broods in 1 yr (Keegan and Crawford 1993).

Hens with broods were monitored ≥ 2 times/wk from May through September during 1989 and 1990. We considered young birds poults until 12 wk of age. We verified brood survival by audio or visual evidence weekly until all poults disappeared or until broods were integrated into autumn flocks.

We ascertained direction to radio signals by the peak-signal method (Springer 1979). Preliminary bearings and signal strength were used to move within 0.5 km of birds; subsequent bearings provided triangulation data. Hens were located by triangulation from ≥ 3 locations or by visual observation. Locations were obtained in 3 approximately equal time periods: morning (0.5 h before sunrise to 4 h after sunrise), midday (4 h after sunrise to 4 h before sunset), and evening (4 h before sunset to 0.5 h after sunset). We located each hen ≥ 1 time during each daytime period in every 2-wk interval. To the extent possible, hens were monitored daily to identify mortality and movements.

Accuracy of telemetry procedures was tested by taking bearings on transmitters at 5 locations from 3 distances encompassing the range of tracking situations. Differences between estimated and actual azimuths were used to calculate error within and among distances and locations. Variances of error angle estimates were not homogeneous among observers and distances. Therefore, standard deviations of error angles were pooled when appropriate and assigned to each triangulation based on observer and estimated distance from transmitter. Mean difference between estimated and true azimuths for all tested observer-distance combinations was 1° ($s_{\bar{x}} = 0.4$). We entered azimuths and receiver locations into program XYLOG (Dodge and Steiner 1986) to process triangulation data. Habitat availability was defined by a minimum convex polygon (Mohr 1947) for all hen locations (except for 2 hens that were excluded because of movements >30 km).

Habitat Mapping and Quantification

We identified 10 cover types from aerial photographs (taken during summer 1989) and ground reconnaissance. Sites ($n = 56$) for quantifying physiographic and vegetative variables were randomly located in all cover types and consisted of 3 points located 30 m apart. Cover types were delineated and descriptions were developed by sampling physiographic characteristics and 4 vegetative strata: overstory (woody plants >3 m tall), midstory (woody plants >3 m tall, but beneath canopy), shrub (woody plants 1–3 m tall), and understory (woody and herbaceous plants <1 m tall).

We quantified physiographic and overstory and midstory vegetative variables at each site: percent slope, aspect, elevation, percent nonforested habitat within 0.3 km, species composition, density, basal area, percent cover, and canopy height. We estimated slope with a clinometer, aspect with a compass, and elevation from topographic maps. Percent nonforested habitat (<10% tree cover) within 0.3 km of each brood-rearing site was estimated from habitat maps with an overlay of 50 randomly distributed points (Marcum and Loftsgaarden 1980). We recorded species, distance to sample point, and diameter-at-breast-height (dbh) of the nearest tree in each "quarter" for midstory and overstory strata to calculate density and basal area (Cottam and Curtis 1956). Percent cover of overstory and midstory strata (combined) was estimated with a sighting tube (James and Shugart 1970) by presence or absence at 2-m intervals along four 10-m transects originating at sample points. We measured heights of 5 randomly selected trees in each stratum with a clinometer to estimate canopy heights.

We quantified the following shrub and understory characteristics at all sample sites: tall shrub cover, understory vegetation height, understory groundcover, and horizontal screening. We estimated tall shrub cover along each of four 10-m transects with the line-intercept method (Canfield 1941). Understory vegetation was sampled in five 1-m^2 circular plots, 1 at the central sample point and 4 at randomly selected points within 4 m. We measured understory vegetation height at 4 random locations in each 1-m^2 plot and estimated percent cover of grasses and grasslike plants, forbs, low shrubs (<1 m), bare ground, and woody debris. A vegetation profile board (0.3 × 1.2 m; Nudds 1977) was placed at sample points and observed from 4 locations at a distance of 10 m (at 0.75 m above ground level) to provide an index of horizontal cover. We estimated percent horizontal screening for each 0.3-m interval on profile boards.

Three nonforested cover types covered 12% of the study area: recent clearcut (<10 yr since harvest), brushfield, and meadow/pasture (Table 1). Savannas were the rarest habitat, typified by scattered trees or clumps of trees that usually had not been managed for timber production. In contrast, timber management likely influenced stand development in hardwood/conifer woodlands (HCW). Remaining cover types were seral or management stages of forested mixed conifer stands. Douglas fir was a prominent component of most stands, but several other conifer species frequently occurred as co-dominants: ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), and incense-cedar (*Calocedrus decurrens*). Dense large/mature mixed conifer (DMC) was the most common cover type, with overstory trees ≥50 cm dbh and >110 yr old. Open large/mature mixed conifer (OMC) often developed from natural or management-related thinning in dense stands. Some OMC stands may have developed following sparse regeneration in areas under even-age management. The second most prevalent cover type was dense medium/young mixed conifer (DYC). Open medium/young mixed conifer stands were rare (<0.2%) and structurally similar to open sapling/pole conifer stands. Therefore, we combined open medium/young mixed conifer stands with open sapling/pole stands. Open sapling/pole/young mixed conifer (OSPC) stands likely developed as a result of sparse regeneration or precommercial thinning. Dense sapling/pole mixed conifer (DSPC) stands resulted from normal tree growth after even-age regeneration harvest or catastrophic disturbance.

Brood-rearing Site Quantification

The steep terrain and dense vegetation of the study area hampered direct observation of undisturbed broods. Therefore, telemetry locations and visual observations of undisturbed broods defined sample sites. We considered hen-poult flocks undisturbed when turkeys were apparently unaware of observer presence or did not alter their activity (e.g., feeding or loafing).

We quantified 2 randomly selected brood-rearing sites each week during 1989 and 1990 brood-rearing seasons (mid-May through mid-September) with the provision that each brood hen was included ≥1 time/season. Each hen with a brood contributed an average of 2.7 measured sites (range 1–7). Although a single hen was randomly selected as a focal hen, gang brooding was a common phenomenon, and brood-rearing sites were occupied by up to 4 radio-marked hens as well as unmarked hens with and without broods.

Vegetative characteristics of brood-rearing habitats were sampled at 3 points, 1 at the observation or triangulation point and 2 located 30 m from the site at random compass bearings. Brood-rearing sites were quantified with the same methods used to develop general cover-type descriptions.

TABLE 1. Descriptions of habitats available to Rio Grande Wild Turkeys in Douglas County, Oregon, 1989–90.

MIXED HARDWOOD/CONIFER

At least 30% hardwoods in canopy layer. Usually dominated by Oregon white oak and Pacific madrone with scattered conifers. All tree size classes present. Understory dominated by bare ground with approximately equal proportions of grasses, forbs, low shrubs, and debris. Poison oak was a common low shrub. Generally at lower elevations (<750 m) on southerly aspects. Included relatively rare riparian zones dominated by Oregon ash and bigleaf maple. Relatively sparse tall shrub cover.

1. Woodland: Stand canopy closure ≥40%; occupied 7% of the area.
2. Savanna: Overall stand canopy closure 10–40%; rarest cover type (2%).

MIXED CONIFER

Less than 30% hardwoods in canopy layer. Most stands were dominated by Douglas fir, but often contained ≥1 co-dominants.

1. Dense large/mature: Overall stand canopy closure ≥70%. Average dbh of overstory conifers ≥50 cm; trees of this size were mature (usually ≥110 yr old). Disturbance, if any, was related to fire, wind, or selective/salvage logging. Characterized by sparse grass cover, large amounts of bare ground, low shrubs, and slash. Most common cover type (49%).
2. Open large/mature: Same size classes as in 1 with canopy closure between 10% and 70%. Stands generally resulted from shelterwood regeneration harvest, commercial thinning, or sparse regeneration. Understory dominated by bare ground and slash; few shrubs, grasses, or forbs. Covered 4% of the area.
3. Dense medium/young: Canopy closure ≥70%. Average dbh of overstory conifers was 23–50 cm; these diameters corresponded to approximate ages of 30–110 yr. Typically, understory vegetation was <10 cm with little grass cover and much bare ground. Occurred on 14% of the area. Virtually all stands in this size class were classified as dense.
4. Dense sapling/pole: Canopy closure ≥70%. Average conifer dbh was <23 cm; trees were usually 10–30 yr old. Grass was scarce, whereas woody plants were dominant in the understory. These stands generally resulted from even-age management such as clearcut or shelterwood regeneration harvests. Found on 8% of the area.
5. Open sapling/pole young: Canopy closure was between 10% and 70%. In most stands overstory dbh was <23 cm. Open stands generally resulted from precommercial thinning or sparse regeneration. There was much variation among stands, but tall understory vegetation and high horizontal screening values were characteristic features. Most forb-rich cover type. In some stands well-developed shrub layers contributed to horizontal screening. Because of structural similarities, open medium/young stands were combined with open sapling/pole stands. Occupied 3% of the area.

BRUSHFIELD

Tree canopy was <10% and hardwood shrub cover was ≥15%. Seral or climax communities dominated by a diverse association of tall shrubs including ceanothus, manzanita, and poison oak. Dense shrub growth provided high horizontal screening. Sparse grass cover and large amounts of bare ground occurred in understories. Commonly occurred on areas that were previously clearcut or burned, particularly where regeneration failed. Included rocky areas with scattered shrubs. Found on 4% of the area.

MEADOW/PASTURE

Natural or management-induced openings with <10% tree canopy. Dominated almost entirely by low grasslike plants, mosses, and bare ground. Shrubs were rare and horizontal screening was low. Coverage of 3% included small pastures and hayfields.

CLEARCUT

Areas where overstory was harvested within 10 yr and generally with <10% tree canopy. Often included seed tree regeneration and shelterwood regeneration after residuals were removed. Bare ground was the most common understory component. Relatively tall understory vegetation dominated by grasses with similar amounts of forbs, slash, and low shrubs (including conifer seedlings). Occupied 6% of the area.

Statistical Analyses

We analyzed data sets with a series of univariate and multivariate procedures. We combined all brood-rearing sites within cover types (based on year, hen age, poult age, and brood fate) because of small sample sizes. All data sets were examined to assess outliers, normality, multicolinearity, and homogeneity of variance-covariance matrices. Although data were variable, we detected few distinct outliers and inclusion of those observations did not alter results. Several variables displayed nonnormal distributions. However, transformations did not improve normality nor alter results, so original values were retained for all analyses. When ≥2 variables were highly correlated ($r > 0.7$), we selected those variables with the greatest ecological relevance or potential for management application that contributed to the most parsimonious description of relationships.

We used analysis of variance to identify variables that differed between groups (e.g., random and brood-rearing sites) and to reduce the number of variables entered in subsequent multivariate procedures. Stepwise discriminant analysis (SAS 1989) was employed to select variable sets to distinguish between groups of observations. We then included variable sets selected in stepwise procedures in canonical analyses of discriminance (SAS 1989) to identify correlations between discriminating variables and canonical functions. Numbers of variables included in these analyses were restricted according to sample size considerations for each group.

Chi-square analysis was used to test the null hypothesis that cover types were used in proportion to availability (Neu et al. 1974, Byers et al. 1984). When the null hypothesis was rejected, we calculated simultaneous confidence intervals to identify which cover types contributed to differences in use and whether use was greater or less than expected. Preliminary analyses indicated that habitat use did not differ with year or hen age for any comparisons. Consequently, observations were pooled for examination of habitat use.

RESULTS

Habitat Use

Hens produced 47 broods and we identified ≥1 brood site for 33 of those broods. We did not locate 14 broods because of radio failure, death of hens, or brood disappearance. We identified cover type at 362 locations of hens with broods <12 wk old ($\bar{x}$ = 11.7 locations/hen, range 1–49), and 64 of these sites were subjected to detailed vegetation sampling. Gang-brooding occurred and sites sometimes were occupied by >1 brood. Hens used 9 cover types for brood rearing (Table 2), and habitat use differed from availability ($P \leq 0.005$). Nearly 50% of brood locations were in the 3 types used more often than expected: HC woodland (27%), meadow/pasture (12%), and HC savanna (8%). Collectively, these cover types represented only 11% of available habitat. Furthermore, when 90% confidence intervals were applied to brood habitat data, use of DYC exceeded availability. Brushfields were not used, and open and dense MC and dense SPC stands were used less than expected ($P \leq 0.05$). Use of clearcuts and OSP conifer stands did not differ from availability.

Habitat Characteristics

Most characteristics of randomly located sites differed among cover types available to wild turkeys (Tables 3–5). Similarly, several differences were apparent among cover types used for brood rearing (Tables 6, 7).

Brood-rearing sites were structurally simple. Mean understory vegetation height at sites was ≤20 cm in all cover types (Table 7). Horizontal screening from ground level to 30 cm ranged from 43% in meadows to 80% in OSP conifer stands, whereas screening in strata above 30 cm rarely exceeded 50%. Tall shrub cover was sparse (≤77 cm/10 m in any cover type). Except in meadows, understory composition at brood-rearing sites was dominated by bare ground (36–57%). We observed considerable variability among proportions of other understory components; grass cover ranged from 7% in OM conifer to 42% at meadow/pasture sites. Forbs, low shrubs, and woody debris each accounted for 7–28% of brood-site understory cover among 8 cover types. However, total understory vegetative cover (grass, forb, and low shrub) at brood-rearing sites was consistent and ranged from 44% to 52% among all cover types except meadow/pasture.

Brood-rearing sites in meadows and pastures (n = 7) were distinguished from random locations by the amount of bare ground. Based on discriminant analysis, we ascertained that group differences explained 70% of variation in the canonical function (P = 0.003). Random sites were characterized by twice as much bare ground as brood sites.

Two variables, overstory tree height and density, in the OSP conifer cover type provided discrimination between brood sites (n = 7) and random locations (P = 0.009). However, only 54% of the function variation was attributed to group differences. Random locations tended to have fewer, shorter overstory trees compared with brood-rearing sites.

Within the DM conifer cover type, midstory tree height, woody debris, and horizontal screening (60–90 cm) discriminated between brood sites (n = 11) and random locations. The canonical function with these variables accounted for 81% of the variation between

TABLE 2. Habitats used for brood rearing by Rio Grande Wild Turkey hens, Douglas County, Oregon, 1989–90 (n = 362 locations associated with 33 broods).

Cover type	Sites (n)	Percent		Bonferroni 95% confidence interval		Selection[a]
		Available	Used	Lower	Upper	
Clearcut	17	6.1	4.7	0.8	8.6	0
Meadow/pasture	44	2.5	12.2	7.1	17.2	+
Brushfield	0	3.8	0	–1.9	1.9	–
Open sapling/pole mixed conifer[b]	8	3.4	2.2	–0.6	5.0	0
Dense sapling/pole mixed conifer	2	8.0	0.6	–2.4	3.5	–
Dense young mixed conifer	76	14.4	21.0	14.0	27.9	0
Dense mature mixed conifer	84	48.9	23.2	15.2	31.2	–
Open mature mixed conifer	5	4.3	1.4	–1.3	4.0	–
Mixed hardwood/ conifer woodland[c]	97	6.8	26.8	19.8	33.8	+
Mixed hardwood/ conifer savanna	29	2.0	8.0	3.8	12.3	+

[a] Where 0 represents use in proportion to availability, + represents greater use of a habitat than expected, and – represents less use of a habitat than expected ($P \leq 0.05$).

[b] In conifer cover types, open defined as canopy closure <70%.

[c] Woodland defined as canopy closure ≥40%; savanna canopy closure was <40%.

TABLE 3. Overstory and midstory characteristics of available habitats in Rio Grande Wild Turkey study area, Douglas County, Oregon, 1989–90.

Cover type[a]	n	Overstory								Midstory							
		Height (m)		Dbh (cm)		Basal area (m^2/ha)		Trees/ha		Height (m)		Dbh (cm)		Basal area (m^2/ha)		Trees/ha	
		$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$
CC	3	4	2	6	3	0.1	0.1	19	10								
MP	3																
B	1	7		5		1.2		356									
OSPC	8	14	1	23	2	5.5	1.3	126	36	5	1	7	1	2	0.5	282	77
DSPC	2	17	3	21	1	11.6	3.5	291	69	7	2	6	0.2	3	0.02	749	38
DYC	11	22	1	30	1	30.8	5.5	396	70	8	1	11	1	10	2.5	1005	250
DMC	15	50	2	82	4	52.4	5.3	100	12	15	1	16	1	16	2.4	545	82
OMC	2	43	11	86	25	14.4	6.8	23	1	10	2	16	2	2	0.4	82	1
HCW	7	16	1	25	3	10.0	1.1	213	31	7	1	9	1	4	1.0	701	153
HCS	4	20	5	33	10	6.5	1.4	130	66	8	1	14	6	2	0.3	294	117

[a] CC = clearcut, MP = meadow/pasture, B = brushfield, OSPC = open sapling/pole mixed conifer, DSPC = dense sapling/pole mixed conifer, DYC = dense young mixed conifer, DMC = dense mature mixed conifer, OMC = open mature mixed conifer, HCW = hardwood/conifer woodland, and HCS = hardwood/conifer savanna.

brood and random sites (P = 0.0001). Random sites had taller midstory trees, more woody debris, and greater horizontal screening than brood-rearing sites.

Twelve brood sites were measured in HC woodlands. Bare ground, forb cover, and midstory tree height discriminated between brood sites and random locations, accounting for 67% of between-group differences (P = 0.0007). Random sites had more bare ground and forb cover and taller midstory trees than brood-rearing sites.

Midstory tree height and grass cover discriminated between random and brood-rearing sites (n = 6) in HC savannas, encompassing 89% of variation in the canonical function

TABLE 4. Characteristics of available habitats in Rio Grande Wild Turkey study area, Douglas County, Oregon, 1989–90.

Cover type[a]	n	Canopy cover (%) $\bar{x}$	Canopy cover (%) $s_{\bar{x}}$	% nonforest within 0.3 km $\bar{x}$	% nonforest within 0.3 km $s_{\bar{x}}$	Elevation (m) $\bar{x}$	Elevation (m) $s_{\bar{x}}$	Slope (%) $\bar{x}$	Slope (%) $s_{\bar{x}}$	Tall shrub cover (cm/10 m) $\bar{x}$	Tall shrub cover (cm/10 m) $s_{\bar{x}}$	Understory height (cm) $\bar{x}$	Understory height (cm) $s_{\bar{x}}$
CC	3	0	0	55	11	937	202	11	3	13	6	22	1
MP	3	0	0	69	15	910	89	8	2	0	0	11	4
B	1	37		48		888		32		73		21	
OSPC	8	36	5	18	12	945	56	17	3	69	24	25	5
DSPC	2	79	7	0	0	928	68	13	1	154	48	16	4
DYC	11	83	4	5	2	710	57	15	2	49	14	9	2
DMC	15	91	3	6	2	808	59	19	3	43	16	15	3
OMC	2	31	9	11	1	1072	74	15	2	1	1	5	2
HCW	7	61	7	15	4	701	36	14	2	34	11	11	2
HCS	4	46	7	1	1	684	78	8	1	31	21	12	3

[a]CC = clearcut, MP = meadow/pasture, B = brushfield, OSPC = open sapling/pole mixed conifer, DSPC = dense sapling/pole mixed conifer, DYC = dense young mixed conifer, DMC = dense mature mixed conifer, OMC = open mature mixed conifer, HCW = hardwood/conifer woodland, and HCS = hardwood/conifer savanna.

TABLE 5. Understory characteristics of available habitats in Rio Grande Wild Turkey study area, Douglas County, Oregon, 1989–90.

		Horizontal screening (%)								Groundcover (%)									
		0–30 cm		30–60 cm		60–90 cm		90–120 cm		Grass		Forb		Bare		Low shrub		Debris	
Cover type[a]	n	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$
CC	3	81	8	60	9	37	10	31	9	25	10	16	5	25	10	17	2	23	4
MP	3	25	10	9	8	3	3	0.3	0.3	36	4	2	1	63	4	0	0	0	0
B	1	96		85		81		83		5		15		33		39		13	
OSPC	8	85	5	76	7	65	9	60	8	14	3	26	5	28	4	22	5	16	4
DSPC	2	98	2	93	6	89	6	86	9	2	1	11	2	43	2	30	11	17	8
DYC	11	73	4	62	4	50	4	51	5	3	2	16	4	51	5	15	3	19	2
DMC	15	72	5	56	5	41	5	37	4	2	1	12	2	39	3	26	3	25	2
OMC	2	51	3	40	3	30	4	22	4	7	5	8	1	50	10	5	2	31	15
HCW	7	60	7	47	7	38	5	40	4	11	2	13	3	58	8	10	3	10	2
HCS	4	59	14	40	14	28	11	30	13	21	9	16	1	41	6	11	6	12	4

[a]CC = clearcut, MP = meadow/pasture, B = brushfield, OSPC = open sapling/pole mixed conifer, DSPC = dense sapling/pole mixed conifer, DYC = dense young mixed conifer, DMC = dense mature mixed conifer, OMC = open mature mixed conifer, HCW = hardwood/conifer woodland, and HCS = hardwood/conifer savanna.

TABLE 6. Overstory and midstory habitat characteristics at Rio Grande Wild Turkey brood-rearing sites, Douglas County, Oregon, 1989–90.

	Clearcut (n = 2)		Meadow (n = 7)		Open SPC[a] (n = 7)		Dense YC (n = 15)		Dense MC (n = 11)		Open MC (n = 3)		HCW (n = 12)		HCS (n = 6)	
Variable[b]	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$
Overstory																
height (m)	30	12	27	3	21*	3	26	1	37	1	40	1.3	19	1	16	1
dbh (cm)	44	17	54	4	31	4	38	2	60	4	80	5	29	3	27	2
basal area (m^2/ha)	9	6	5	2	10	3	20	3	29	4	17	9	12	1	4	1
density (no./ha)	37	1	17	4	175*	95	166	22	96	14	28	13	189	36	61	12
Midstory																
height (m)	10	4	9	1	7	1	9	0.5	10*	0.5	9	2	6*	0.3	6*	0.4
dbh (cm)	13	7	17	2	9	2	11	1	12	1	12	3	9	1	9	1
basal area (m^2/ha)	3	3	1	0.4	3	1	7	2	8	1	1	0.5	5	1	1	0.3
density (no./ha)	101	28	44	21	268	123	493	95	580	99	59	7	594	162	156	28
Canopy cover (%)	25	20	32	9	45	7	71	4	69	5	23	12	67	3	30	5
Elevation (m)	570	5	658	35	658	106	603	30	524	20	653	56	580	20	586	39
Slope (%)	11	3	15	2	16	2	13	2	15	2	18	5	12	1	11	3
Nonforest within 0.3 km (%)	9	1	14	3	6	2	6	1	3	1	3	2	5	1	6	2

[a]SPC = sapling/pole conifer, YC = young conifer, MC = mature conifer, HCW = hardwood/conifer woodland, HCS = hardwood/conifer savanna.
[b]Variable means followed by an asterisk were selected by stepwise discriminant analysis when compared to randomly located sites within the same cover type.

TABLE 7. Understory habitat characteristics at Rio Grande Wild Turkey brood-rearing sites, Douglas County, Oregon, 1989–90.

	Clearcut (n = 2)		Meadow (n = 7)		Open SPC[a] (n = 7)		Dense YC (n = 15)		Dense MC (n = 11)		Open MC (n = 3)		HCW (n = 12)		HCS (n = 6)	
Variable[b]	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$
Tall shrub cover (cm/10m)	9	9	13	7	67	15	48	11	77	13	12	3	50	12	12	3
Horizontal screening (%)																
0–30 cm	44	9	43	5	80	6	67	5	71	3	65	11	57	5	63	5
30–60 cm	23	3	22	5	69	6	50	5	53	4	47	11	43	5	36	6
60–90 cm	11	6	12	4	54	6	36	4	38*	4	26	5	34	5	22	4
90–120 cm	13	10	12	5	51	7	36	4	36	4	23	6	38	5	21	3
Understory height (cm)	5	2	15	2	20	3	15	2	15	1	12	4	13	1	18	3
Understory cover (%)																
Grass	8	6	42	7	8	2	10	3	12	3	7	2	17	3	37*	8
Forb	12	1	18	4	28	2	15	2	16	3	22	6	10*	2	12	1
Bare	57	15	28*	5	37	5	40	4	36	3	43	15	48*	4	38	8
Low shrub	8	6	10	2	18	4	23	4	27	2	11	3	18	3	11	3
Debris	19	14	7	3	15	4	17	2	13*	2	22	8	9	2	7	2

[a]SPC = sapling/pole conifer, YC = young conifer, MC = mature conifer, HCW = hardwood/conifer woodland, HCS = hardwood/conifer savanna.
[b]Variable means followed by an asterisk were selected by stepwise discriminant analysis when compared to randomly located sites within the same cover type.

(P = 0.0004). Midstory tree height followed the same trend noted in HC woodlands (higher values at random sites); grass cover was greater at random sites compared with sites used by broods.

Broods were most often found on southeast slopes, and those aspects were used more than expected ($P < 0.01$). All north-facing slopes were used less than expected for brood rearing ($P < 0.01$); southwest slopes were used in proportion to availability.

DISCUSSION

Habitat Use

Comparisons of brood habitat use among Rio Grande Wild Turkey populations were difficult because of the scarcity of quantitative evaluations in other regions or the relative simplicity of vegetation where other populations existed. For example, Schmutz et al. (1990) delineated only 3 habitats for an introduced Rio Grande Turkey population in northeastern Colorado. Our results were similar to those of Mackey (1986) for Merriam's Wild Turkey (*M. g. merriami*) broods in Washington where oak and oak-pine habitats were used more than expected, but only 2 other cover types were available. Our results also supported findings of Rumble and Anderson (1993) for Merriam's Turkeys in South Dakota; brood hens in both populations used meadows more than expected and dense conifer stands less than expected. We hypothesize that Rio Grande brood use of cover types was influenced by habitat patchiness, particularly in dense mature conifer stands. For example, less debris, less canopy cover, and more grass cover at brood-rearing sites in DMC stands probably indicated use of small openings or parklike areas in otherwise dense stands. Use of small openings (<1 ha) within larger forest tracts was noted for Merriam's Turkeys in Washington (Mackey 1986). Rumble and Anderson (1993) reported that hens with poults <12 wk old rarely moved >10 m into meadows. Similarly, we saw few broods near centers of large openings until poults were ≥3 months old.

Our findings coincided with patterns of habitat use summarized by Porter (1992). Savannas and open woodlands provided brood-rearing habitat, and these cover types were used more than expected by Rio Grande Wild Turkey hens with broods in southwestern Oregon. We interpreted observations of hens with broods in a number of habitats as evidence that hens made use of a range of conditions available in several cover types. However, we recognized that we could not ascertain specific activities associated with some locations, and measured sites may have represented a blend of areas used for several reasons (e.g., food, rest, or escape).

Habitat Characteristics

Descriptions of specific brood-site characteristics for Rio Grande Turkeys in native range were lacking; however, brood-rearing habitats used by other subspecies were described as parklike (Porter 1992). Our observations were consistent with previous observations throughout many parts of the country, but tended to represent the low end of the range of vegetative cover values. The relatively open character of sites occupied by brood hens probably allowed for greater poult mobility and foraging opportunity and reduced contact with wet vegetation. Conversely, sites typified by heavy slash concentrations and dense understory vegetation (e.g., >80% horizontal screening from 0 to 1.2 m) probably were used little because poult mobility and hen vision were restricted. Mackey (1986) speculated that dense vegetation conditions limited use of some sites in Washington.

Structural characteristics of sites used by Rio Grande hens with broods were different from those described by Mackey (1986) for Merriam's Turkeys and by Schmutz et al. (1990) for Rio Grande Turkeys in Colorado. Merriam's and Rio Grande brood sites outside Oregon were composed of taller understory vegetation (44 cm) than we found in southwestern Oregon (15 cm). We also observed different trends in total understory cover and horizontal screening compared with other areas. Merriam's brood sites (Mackey 1986) had greater screening than random sites. Average horizontal screening was moderate (33–64%) at Rio Grande brood-rearing sites in Oregon, but little different from random locations. By contrast, total understory vegetation cover at Washington brood sites (34%) was less than at random sites (Mackey 1986), but total cover was higher at brood-rearing sites (52%) than at random sites in Oregon.

Schmutz et al. (1990) found more grass cover at some Rio Grande brood sites, similar to that in southwestern Oregon, but Day et al. (1991)

noted less grass cover at some brood sites than at random locations (however, available grass cover in study areas outside Oregon was much higher than that in southwestern Oregon). Like Schmutz et al. (1990), we did not observe differences in sites used by different age broods, nor did we record consistent differences between brood-rearing sites and random locations. Rather, Rio Grande brood-rearing sites in Oregon encompassed a variety of plant associations and structures but were within ranges observed in other parts of wild turkey range. Southeast slopes provided poults with the best opportunities for feeding and easy travel because these slopes dried quickly each day and supported cover types used most by brood hens.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Our research indicates that Rio Grande Wild Turkey broods in the southern Oregon Cascades use a variety of cover types and a range of conditions within cover types. Because they use most available cover types for brood rearing, Rio Grande Turkeys would probably thrive under a variety of habitat conditions, including some not considered typical wild turkey habitat. However, before selecting sites for translocation, managers should consider the types of habitat available and likely future land-management scenarios. Esthetic and economic returns of translocation programs will be enhanced by selection and prioritization of sites best suited to wild turkey brood-rearing habitat needs.

Although Rio Grande Turkeys use a variety of habitats successfully, several management practices would enhance brood habitat. Only dense stands resulting from recent perturbations (conifer or tall shrub stands that developed after even-age management practices or disturbance) received little use. When compatible with other objectives, we hypothesize that prescribed burning (e.g., in brushfields) or patch thinning (e.g., in dense sapling/pole stands) to reduce excessively dense vegetation (to <25% low shrub cover and <25 cm vegetation height) would likely increase wild turkey use, particularly in areas where brood habitat is limited. Maintaining areas of mixed hardwood/conifer cover types (particularly oak woodland and savanna complexes) would ensure availability of brood-rearing habitat. Turkeys would also benefit from conservation and enhancement of openings and parklike areas in conifer cover types, particularly in areas with low hardwood/conifer stand abundance or distribution.

Because dense mature conifer was used less than expected for brood rearing, Rio Grande Turkeys may be able to utilize landscapes dominated by relatively young forests (30–110 yr old and 23–50 cm dbh). However, dense mature conifer received heavy use for most components of turkey life history (e.g., ranked second for brood habitat use and first for hen-poult roosts [Keegan 1996]). Therefore, we do not recommend extensive harvest of mature timber as a means of increasing wild turkey numbers.

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DISTRIBUTION OF THE MILLIPED *TYLOBOLUS UTAHENSIS* CHAMBERLIN, WITH REMARKS ON *T. FREDERICKSONI* (CAUSEY) (SPIROBOLIDA: SPIROBOLIDAE)

Rowland M. Shelley[1] and Selena B. Bauer[1]

ABSTRACT.—*Tylobolus utahensis* Chamberlin, the only representative of the genus occurring in the southwestern deserts, ranges from central Inyo County, California, to the western periphery of Kane County, Utah. This distribution roughly corresponds to the northern limit of the Mojave Desert ecosystem and is also shown by the milliped *Piedolus utus* Chamberlin (Spirobolida: Atopetholidae) and the centipede *Theatops posticus* (Say) (Scolopendromorpha: Cryptopidae). *Tylobolus fredericksoni* Causey, ostensibly from Douglas County, Kansas, is designated a "*nomen dubium*" and disregarded pending collection of fresh material; *Narceus gordanus* (Chamberlin) is deleted from South Carolina and Tennessee. *Tylobolus uncigerus* (Wood) occurs north of the Columbia River in Klickitat County, Washington, and *Hiltonius thebanus* Chamberlin is referrable to *Onychelus* Cook in the family Atopetholidae.

Key words: Tylobolus; T. utahensis; T. fredericksoni; Narceus americanus; *Washington County, Utah; Inyo County, California;* Hiltonius.

The subfamily Tylobolinae of the diplopod family Spirobolidae comprises 2 genera, *Tylobolus* Cook and *Hiltonius* Chamberlin. Keeton (1960) revised both taxa, recognizing 3 species of *Hiltonius* in southwestern California and adjacent Baja California Norte, and 2 species in mainland Mexico that range northward into Santa Cruz County, Arizona (Keeton 1960, Shelley 1995, plus unreported samples examined by the 1st author). The 6th species, *H. thebanus* Chamberlin, occurring at Theba, Maricopa County, Arizona, is referrable to *Onychelus* Cook in the family Atopetholidae, as the 1st author has learned from examining the female holotype at NMNH (see acronyms below). In a supplemental paper on the California representatives of *Tylobolus*, Keeton (1966) cited 6 species west of the crest of the Sierra Nevada, 1 of which, *T. uncigerus* (Wood), ranged northward to the Columbia River at Portland, Oregon; we extend its distribution into the adjacent periphery of Washington based on a male and female from Klickitat, Klickitat County, at FSCA. *Tylobolus* extends southward into the adjacent fringe of Baja California Norte (Bollman 1888, Keeton 1960, Loomis 1968) and, like *Hiltonius*, occupies the western interior, as *T. utahensis* Chamberlin inhabits Zion National Park, Washington County, Utah. There are also questionable reports of an additional species, *T. fredericksoni* (Causey), in Douglas County, Kansas, on the eastern periphery of the Central Plains. We report 37 additional samples of *T. utahensis* that expand its range some 300 mi (480 km) westward to central Inyo County, California, east of the Sierras, and provide data on segment numbers, lengths, and widths. We also designate *T. fredericksoni* as a "*nomen dubium*" because there is no recent, indisputable evidence that a representative of this genus occurs east of the area occupied by *T. utahensis*. The distribution of the Tylobolinae in the United States and the adjacent periphery of Mexico is shown in Figure 1. Acronyms of sources of preserved study material are as follows:

BYU—Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT
CAS—California Academy of Sciences, San Francisco
CDFA—California Department of Food and Agriculture, Sacramento
DC—Life Sciences Division, Dixie College, St. George, UT
FSCA—Florida State Collection of Arthropods, Gainesville
LACMNH—Los Angeles County Museum of Natural History, Los Angeles, CA

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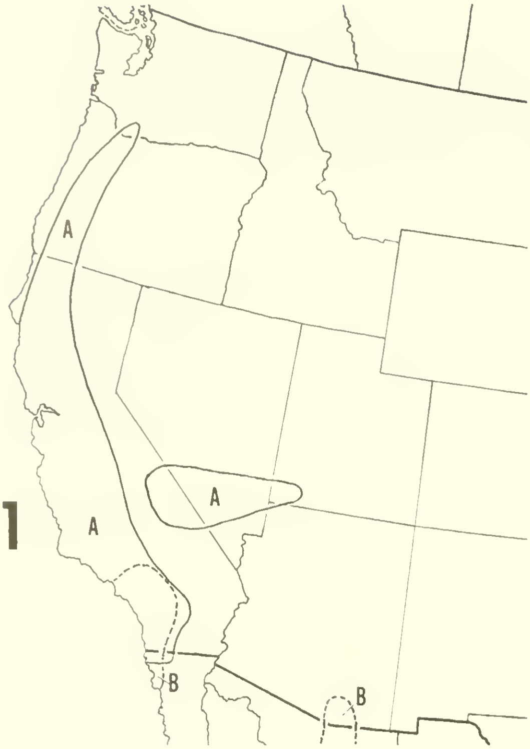


Fig. 1. Distribution of the Tylobolinae in the United States and adjacent periphery of Mexico. Solid lines (A), *Tylobolus;* dashed lines (B), *Hiltonius.*

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA
NCSM—North Carolina State Museum of Natural Sciences, Raleigh
NMNH—National Museum of Natural History, Smithsonian Institution, Washington, DC
SEM—Snow Entomological Museum, University of Kansas, Lawrence
UCD—Bohart Entomological Museum, University of California at Davis
UGA—University of Georgia Museum of Natural History, Athens.

Tylobolus utahensis Chamberlin

(Figs. 2–5)

Tylobolus utahensis Chamberlin, 1925:60–61. Keeton, 1960:131–132, figs. 262–264.
Californibolus utahensis: Chamberlin, 1949: 166. Chamberlin and Hoffman, 1958:162.

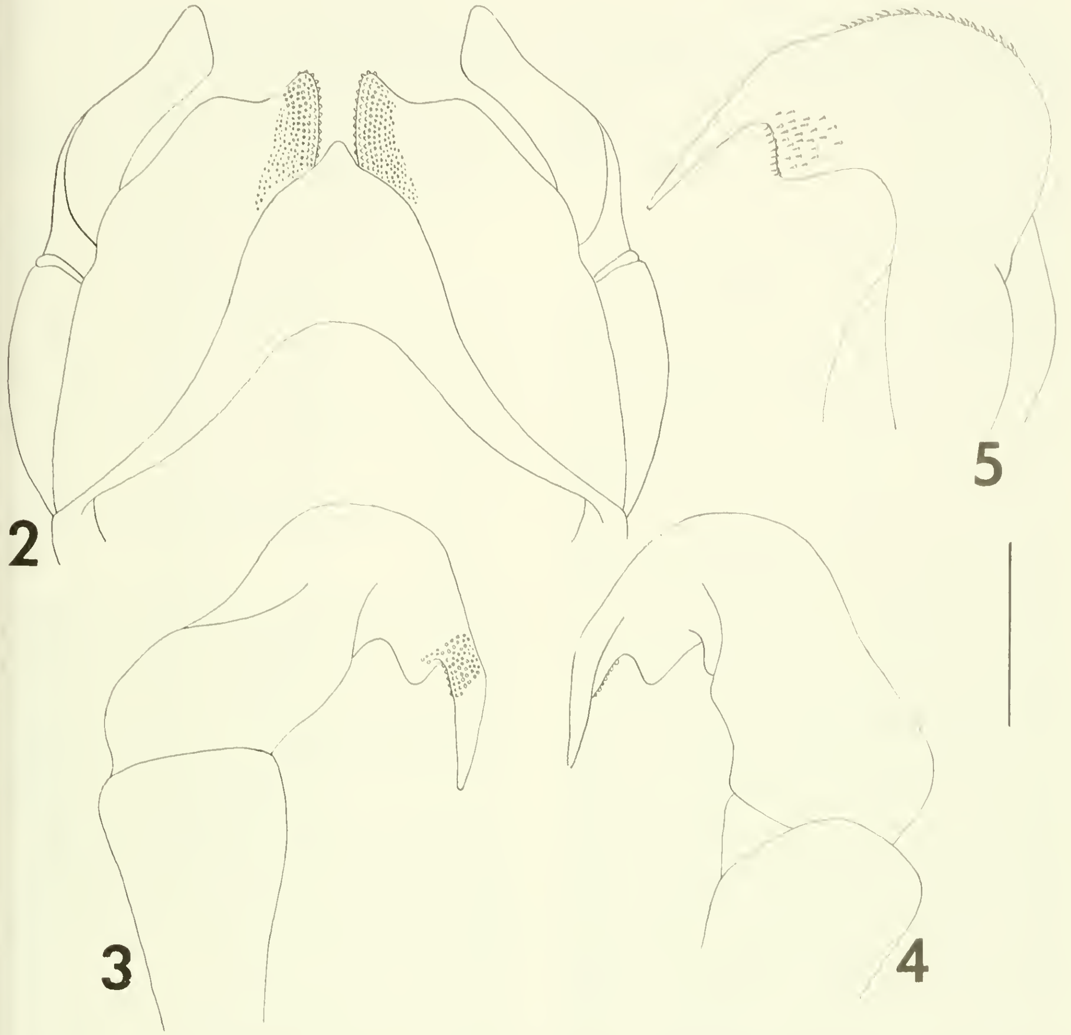
TYPE SPECIMENS.—Male holotype, female allotype, and 2 male and 1 female paratypes (MCZ) collected by R.V. Chamberlin in May 1924 at an unknown location in Zion National Park, Washington County, Utah.

DIAGNOSIS.—Metazonal striae terminating ventrolaterad, well below level of ozopores; anterior gonopod telopodite apically blunt and rounded, not uncinate; posterior gonopod tibiotarsus forming right angle with distal projection (Figs. 2–4).

VARIATION.—New material agrees closely with the holotype. The posterior gonopod tibiotarsus is slightly broader and blunter, and the denticles, which Causey (1955) and Keeton (1960) termed "prickles," cover larger areas on both the anterior and posterior gonopods. In juveniles the distal projection of the posterior gonopod is less angular, extending submediad rather than downward or dorsad. We reexamined the holotype and found the denticles to be stronger than shown by Keeton (1960, figs. 262–264); there is also a pronounced line or ridge of these along the ventral surface of the posterior gonopod telopodite that he did not show (Fig. 5).

In his supplemental work on California species, Keeton (1966) tabulated meristic and morphometric data; we present such data for *T. utahensis* (Table 1) to provide parallel accounts for all species of *Tylobolus.* On the average, females are slightly longer and broader than males; adults are equivalent in length throughout the range, but those on the east are narrower. The adult segment number varies from 51 to 57, as all individuals with ≥ 52 segments have no legless segments except the epiproct. Three females and 2 males have 51 segments, none legless, while 3 males and 1 female with this count have 1 or 3 legless segments; all individuals with ≤ 50 segments have at least 1 without appendages.

DISTRIBUTION.—Occurring from the Inyo Mountains on the eastern side of Owens Valley, Inyo County, California, to the eastern edge of Zion National Park in western Kane County, Utah, a distance of approximately 300 mi (480 km; Figs. 1, 6). The milliped should also be expected along the Virgin River in the northwestern corner of Mohave County, Arizona; along this river and in other parts of northern Clark County, Nevada; and throughout most of Lincoln County, Nevada, particularly in canyons and gorges east of Caliente, Panacea, and Pioche. Specimens in Inyo County were taken in pitfall traps at elevations



Figs. 2–5. *Tylobolus utahensis:* 2, anterior gonopods of a male from Saline Valley, Inyo County, California, anterior view; 3, left posterior gonopod of the same, anterior view; 4, the same, caudal view; 5, right posterior gonopod of holotype, anterior view. Scale line = 1.00 mm for all figures.

of 2296–6560 ft. In addition to the types, specimens were examined as follows:

CALIFORNIA: Inyo Co., Inyo Mts, Lead Canyon (Cyn), F, 9 March–13 August 1981, D. Giuliani (CAS); Inyo Mts, Hunter Cyn, M, F, 9 June 1980–26 May 1981, D. Giuliani (CAS); Inyo Mts, Willow Cr, F, 16 September 1976, collector unknown (LACMNH); Saline Valley, 11 different stations but exact locations unknown, 10M, 17F, juv, 5 April 1959–14 June 1960, B. Banta (CAS); Saline Valley, 10 stations along Grapevine Cyn Rd but exact locations unknown, 16M, 6F, 15 August 1959–7 May 1960, B. Banta (CAS); 21 and 25 mi (33.6 and 40 km) S Saline Valley, 2M, 29 April 1975, A.R. Hardy (CDFA); and Death Valley Nat Pk, Panamint Mts, Johnson Cyn, F, 2 June 1961, R. Waner (NMNH).

NEVADA: Nye Co., Nuclear Test Site, Ranier Mesa, 2M, juv, date unknown, D.B. Thomas (LACMNH, NCSM).

UTAH: Washington Co., 12 mi (19.2 km) NW St. George, nr Baker Dam, 3M, 2F, 16 April 1971, B.K. Carrell (DC); Pine Valley, F, 26 May 1971, Prothero (DC); Snow Cyn St Pk, M, 16 April 1982, R.W. Baumann (BYU); Pintura, F, 8 March 1941, J. & W. Ivie (NMNH); Motaqua, M, 17 April 1933, M. Zuie (NMNH); Oak Grove

TABLE 1. Meristic and morphometric data on *Tylobolus utahensis*. Individuals are listed in descending order according to segment counts, which include the epiproct; the number of legless segments in addition to the epiproct, if any, is shown in parentheses. Measurements are in mm. Averages are for specimens with no additional legless segments.

	Males			Females		
	Segments	Length	Max. width	Segments	Length	Max. width
CA, Hunter Canyon	51(1)	41.7	4.0	49(1)	35.8	3.9
CA, Lead Canyon				50(2)	27.4	3.1
CA, Willow Creek				51(3)	36.1	3.4
CA, Saline Valley	57	70.3	5.1	55	86.7	8.3
″ ″	55	73.8	5.6	55	48.8	5.6
″ ″	55	72.7	7.0	54	76.4	7.4
″ ″	55	67.2	7.2	54	71.4	6.6
″ ″	55	62.8	6.8	54	65.5	6.6
″ ″	54	62.6	6.8	54	64.9	7.2
″ ″	54	59.3	6.0	54	62.3	6.6
″ ″	53	65.1	6.8	54	61.2	7.6
″ ″	53	54.2	5.5	53	74.2	8.2
″ ″	53	48.8	5.6	53	71.0	6.1
″ ″	52(1)	46.2	5.1	53	60.8	6.7
″ ″	52	64.8	6.5	51	47.1	5.3
″ ″				51	46.1	5.5
				46(4)	22.6	2.8
Averages		63.8	6.7		64.4	6.7
CA, Grapevine Canyon Road	55	60.3	5.9	56	65.2	7.7
″ ″	55	59.6	6.2	56	50.6	5.2
″ ″	55	59.1	5.7	54	72.0	7.6
″ ″	55	48.0	5.2	54	63.8	6.7
″ ″	54	60.4	6.1	53	66.8	7.9
″ ″	54	56.1	6.0	53	64.6	6.9
″ ″	54	55.0	6.2	52	56.3	5.9
″ ″	53	77.8	6.7			
″ ″	53	56.4	6.1			
″ ″	52	68.9	7.1			
″ ″	52	58.3	7.0			
″ ″	52	57.8	6.3			
″ ″	52	57.6	6.0			
Averages		59.6	6.2		62.8	6.8
NV, Ranier Mesa	53	59.2	5.7			
UT, Zion National Park	53	62.1	5.3	53	54.8	4.7
″ ″	52	67.5	5.5	52	76.9	6.7
″ ″	52	66.8	5.5	52	71.5	6.7
″ ″	52	65.3	5.6	52	48.8	4.1
″ ″	52	48.8	4.1	51	64.3	6.2
″ ″	51	67.5	5.8			
″ ″	51	49.1	4.5			
″ ″	51(3)	36.5	3.5			
″ ″	51(3)	31.2	3.1			
Averages		61.0	5.2		63.3	5.7

6

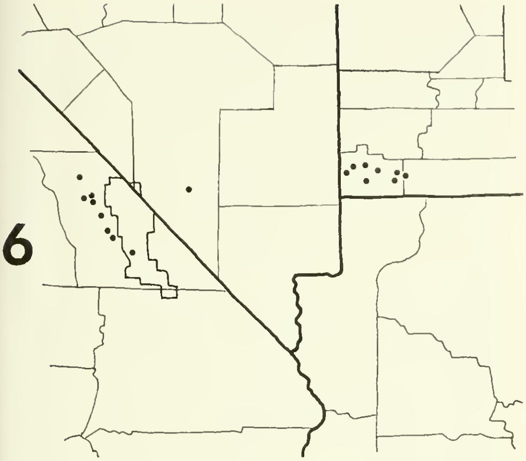


Fig. 6. Distribution of *Tylobolus utahensis.*

Cpgd, F, 2 June 1988, L.L. Smithee (BYU); and Zion Nat Pk, exact site unknown, MM, FF, May 1924, V.M. Tanner (NCSM), 3F, 1927, A.M.U. (NMNH), M, July 1931, W.J. Gertsch (NMNH), and behind visitor's center, F, 30 April 1991, C.S. Crawford (NCSM). Kane Co., Zion Nat Pk, east entrance, M, 3 March 1967, G.F. Knowlton (NMNH).

REMARKS.—*Tylobolus utahensis* demonstrates 2 important distribution patterns among North American myriapods. The occurrences of the genus and subfamily in coastal California and southwestern Utah are reiterated by the tribe Tynommatini and subfamily Tynommatinae in the callipodoid family Schizopetalidae, as *Tynomma* Loomis occurs around San Francisco/San Pablo and Monterey bays, and *Idrionaria* Shelley inhabits Washington County, Utah (Shelley 1996). Secondly, 2 millipeds and 1 centipede are now known to occur between central Inyo County, California, and Washington County, a range that corresponds roughly to the northern limit of the Mojave Desert ecosystem. The other milliped is *Piedolus utus* Chamberlin (Spirobolida: Atopetholidae), which was previously known only from St. George, Washington County (Hoffman and Orcutt 1960), but can now be recorded from Inyo County based on 2 males from Panamint Springs (UCD). Similarly, the scolopendromorph centipede, *Theatops posticus* (Say) (Cryptopidae), occurs in Saline Valley; the Nuclear Testing Site, Nye County, Nevada; and St. George, Utah (Shelley 1990, 1997). Two additional millipeds that may demonstrate this pattern are *Californiulus blechrostriatus* Shelley and Bauer (Julida: Paeromopodidae), occurring in Saline Valley and along the eastern slope of the Sierra Nevada (Shelley and Bauer 1997), and *Idrionaria dineh* Shelley, known only from Washington County (Shelley 1996).

Tylobolus fredericksoni (Causey)

Spirobolus uncigerus Wood: Cragin, 1885:145. Kenyon, 1893:16.
Tylobolus uncigerus: Gunthorp, 1913:164; 1921:88.
Californibolus fredericksoni Causey, 1955:78, 80, figs. 1c, 4–5. Chamberlin and Hoffman, 1958:161.
Tylobolus fredericksoni: Keeton, 1960:132–133.

For over a century records have existed of a mysterious tyloboline on the eastern periphery of the Central Plains. The confusion began with Cragin (1885), who reported *Spirobolus "uncigerus* Wood (?)" from Topeka, Shawnee County, Kansas, stating that there were "important differences" with *uncigerus*, but the specimen was closer to this species than to any other. Kenyon (1895) repeated Cragin's citation, including the parenthetical question mark, for an individual from Weeping Water, Cass County, Nebraska. He also reported the abundant east-Nearctic spirobolid, *Narceus americanus* (Beauvois) [cited as *Spirobolus marginatus* (Say)], from adjacent Sarpy County. Thus, Kenyon's record of *uncigerus* is plausibly a misidentification of this common species. Gunthorp (1913, 1921) questioned Cragin's record as being geographically improbable and deleted *uncigerus* from the Kansas fauna; he suggested that mutilated specimens of *N. americanus* from Topeka [cited as *Arctobolus marginatus* (Say)] may have been misinterpreted. Thirty-four years later Causey (1955) proposed *Californibolus fredericksoni* for 2 males ostensibly collected in 1949 in Douglas County, Kansas, and an immature female taken in 1950 from Monroe County, Iowa. Her illustrations of the anteroventral corner of the mandible and both pairs of gonopods resemble the conditions in *uncigerus*, and all other Kansas spirobolids that she examined were *N. americanus* (cited as *N. oklahomae* Chamberlin). Keeton (1960) examined the holotype, transferred *C. fredericksoni* into *Tylobolus*, and noted that the vial contained fragments of 2 specimens, the anterior end of a small male and the caudal end of a larger individual. As the gonopods appeared to be from an immature specimen, Keeton withheld commentary on the status of *T. fredericksoni* pending discovery of an adult male. In our reexamination of the holotype, we found what appeared to be 1 highly fragmented specimen with no legless segments at the caudal end. Its gonopods are accurately figured by Causey and Keeton and are open to different interpretations. Keeton (1960) thought they were incompletely developed but gave no explanation for this opinion. They seem mature to us, and while similar to those of *T. uncigerus* and plausibly representing a variant, they also show enough differences to be reasonably interpreted as representing a distinct species.

Today, 47 yr after its description, *T. fredericksoni* is still questionable, and no potential tylobolines have been collected from Kansas, Nebraska, or Iowa during this time. Its ostensible occurrence in the Central Plains continues to generate confusion, as Enghoff (1995, family-clade no. 13) recorded *Tylobolus* from the east- and west-Nearctic based on this species. To our knowledge, the only definite spirobolid records from Kansas are of *N. americanus* (cited as *N. oklahomae* Chamberlin) from Douglas County (Causey 1955) and *N. annularis* Rafinesque from Osage County (Keeton 1960). We have seen 1 authentic Kansas spirobolid, a juvenile from Lawrence, Douglas County (UGA), that is clearly referrable to *Narceus.* Aside from south Texas, which is occupied by *Anelus richardsoni* (Pocock) (Allopocockiidae) and 1 or more representatives of the Atopetholidae (Hoffman and Orcutt 1960, Shelley and Hoffman 1995), only 4 spiroboloids definitely occur in the United States east of the Rocky Mountains: *N. americanus*, which is widespread east of the Central Plains and extends northward into Québec (Shelley 1988); *N. gordanus* (Chamberlin), in peninsular Florida[2]; *Chicobolus spinigerus* (Wood) (Spirobolidae), ranging from southern South Carolina to the south Florida Keys (Keeton 1960); and *Floridobolus penneri* Causey (Floridobolidae), endemic to the Lake Wales Ridge, Highlands and Polk counties, Florida (Causey 1957, Keeton 1959, 1960, Deyrup and Franz 1994). There is no recent, credible evidence that another form exists in the eastern two-thirds of the continent, and the locality of *T. fredericksoni* may represent a labeling error. The distribution pattern of species along the Pacific Coast and in the western interior, and another some 1000 mi (1600 km) to the east in the eastern Central Plains, is not demonstrated by another diplopod genus and thus seems implausible for *Tylobolus.* We therefore designate *T. fredericksoni* as a "*nomen dubium*" and recommend disregarding the species until its presence in the Plains is confirmed by a freshly collected male with unimpeachable locality data, or until the milliped is discovered in the principal generic area, probably in California, and an accurate locality can be reported.

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[2] Keeton (1960) recorded females of *N gordanus* from Carter County, Tennessee, and Charleston County, South Carolina, but the 1st author has found only *N. americanus* in these areas. Authentic samples of *N gordanus*, with adult males, have been taken in peninsular Florida from Alachua and St. Johns counties southward. Consequently, we delete *N gordanus* from Tennessee and South Carolina.

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CONTRASTING MOVEMENT AND ACTIVITY OF LARGE BROWN TROUT AND RAINBOW TROUT IN SILVER CREEK, IDAHO

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ABSTRACT.—Recent radiotelemetry studies demonstrated that stream-dwelling trout are mobile, but few have compared sympatric species. We used radiotelemetry to simultaneously monitor positions of 20 brown trout and 21 rainbow trout from May or June 1994 to February 1995 in Silver Creek, a small spring-fed stream in south central Idaho. Our biweekly observations from May to September indicated that rainbow trout had larger home ranges (medians, 606 m v. 131 m) and moved greater distances (medians, 1109 m v. 208 m) than brown trout. Furthermore, rainbow trout used more positions than brown trout (means, 7 v. 3) over this interval. Hourly diel monitoring revealed no significant difference in 24-h home ranges of rainbow trout and brown trout (means, 77 m v. 105 m). However, activity patterns of the 2 species differed; rainbow trout activity was usually highest during the day, whereas brown trout activity tended to peak at night. Differences in foraging strategies and response to disturbance may be responsible for differences in mobility.

Key words: diel activity, home range, movement, brown trout, Salmo trutta, *rainbow trout,* Oncorhynchus mykiss.

Until recently stream-dwelling trout often were considered relatively sedentary, with home ranges <50 m (Gerking 1959, Northcote 1992). Rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) were thought to exemplify this pattern (Klein 1974, Solomon and Templeton 1976, Hesthagen 1988). In part because of the advent of radiotelemetry, stream trout mobility has received greater notice, and seasonal movement may be more prevalent than previously believed (Gowan et al. 1994). For example, mean summer/fall home range of very large (>435 mm) brown trout exceeded 4.9 km in the Au Sable River in Michigan (Clapp et al. 1990), median summer home range of large (>340 mm) brown trout was >400 m in North Platte River tributaries in Wyoming (Young 1994), and median home range of small (<240 mm) Colorado River cutthroat trout (*O. clarki pleuriticus*) was 233 m in a small Wyoming stream (Young 1996). No seasonal radiotelemetry study of rainbow trout in streams has been reported.

Most movement studies have focused on long temporal scales, i.e., movement over weeks, seasons, or years (Miller 1957, Mense 1975, Riley et al. 1992). But distances moved within a diel period have been largely overlooked (but see Clapp et al. 1990). Trout movement may vary between day and night due to changes in light intensity, prey availability, and water temperature. Other behaviors change during the diel cycle. Campbell and Neuner (1985) and Hill and Grossman (1993) noted that rainbow trout move inshore and become less active at night, and feeding by rainbow trout apparently declines at night (Angradi and Griffith 1990). Brown trout were reported to feed primarily in the evening (Elliott 1973) or during the day (Bachman 1984). Clapp et al. (1990) noted that large (>430 mm) brown trout tend to be more active at night, but patterns fluctuated monthly.

There are few comparisons of diel and seasonal mobility of sympatric salmonids. Bjornn and Mallet (1964) evaluated movements of rainbow trout, westslope cutthroat trout (*O. c. lewisi*), and bull trout (*Salvelinus confluentus*) in the Middle Fork Salmon River, Idaho, but results were based on angler recoveries of tagged fish over several years. Matthews et al. (1994) used radiotelemetry to monitor diel changes in rainbow trout and brown trout habitat use, but monitoring lasted only a month and only 1 brown trout was tagged.

Our objectives were to examine rainbow trout and brown trout position changes from late May to early February and to compare their movement and activity over several diel periods in a small stream with naturalized populations.

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STUDY AREA

Silver Creek is a spring-fed tributary of Little Wood River on the northern edge of the Snake River plain, south central Idaho. Mean monthly discharge for 1994 ranged from 1.7 $m^3 \cdot s^{-1}$ in September to 5.1 $m^3 \cdot s^{-1}$ in March. Discharge increased in autumn after irrigation of farmlands ended. Stream gradient of the study area is 0.8–1.0 $m \cdot km^{-1}$ and stream width is 15–30 m. Aquatic macrophytes, especially *Chara vulgaris* and *Potamogeton* spp., are abundant in summer, and silt is the predominant substrate, with areas of gravel and marl. Much of the riparian habitat consists of dense, overhanging stands of willow (*Salix* spp.) and birch (*Betula* spp.). Other fish species are brook trout (*Salvelinus fontinalis*), mountain whitefish (*Prosopium williamsoni*), bridgelip sucker (*Catostomus columbianus*), redside shiner (*Richardsonius balteatus*), longnose dace (*Rhinichthys cataractae*), speckled dace (*Rhinichthys osculus*), Paiute sculpin (*Cottus beldingi*), and Wood River sculpin (*Cottus leiopomus*; Wilkison 1996).

We investigated trout movement in 2 noncontiguous reaches of Silver Creek. The upper reach is 4.1 km long and largely on a Nature Conservancy preserve where angling is permitted but no harvest allowed. The lower reach is 5.1 km long, and harvest is state regulated; 2 fish <305 mm or >406 mm can be kept. An intervening 3.8-km reach was periodically visited to determine presence of fish with transmitters.

METHODS AND MATERIALS

We collected rainbow trout (mean total length [TL] 419 mm, range 357–475 mm, n = 21) and brown trout (mean TL 494 mm, range 342–622 mm, n = 20) by angling or electrofishing and implanted transmitters on 13–15 May and 12–14 June 1994. We surgically implanted sealed, coiled-antenna transmitters in anesthetized fish in the body cavity immediately anterior to the pelvic girdle and released fish at or near the point of capture after recovery (see Young 1995 for details). We monitored fish by radiotelemetry until early February 1995. Only healthy fish were implanted.

To define the longitudinal position of each telemetry location, we staked the bank at 50-m intervals on a line parallel to the thalweg. Fish initially were located from a canoe, then from the stream bank where we measured distance to the nearest stake. Fish were generally located once or twice every 2 wk May–September, once or twice each month in October, November, and December, and once on 9 or 10 February 1995.

Diel observations of fish activity and movement began on 22 June, 12 July, 17 August, and 23 September. Groups of up to 7 fish (up to 4 fish per species) were monitored for 24 h. All positions were identified from the bank, and observers did not disturb fish. We attempted to monitor each fish every hour for at least 1 min, and longer if a fish was active. Number of fluctuations per minute in transmitter signal strength was used as an index of activity (Clapp et al. 1990); fluctuations resulted from changes in transmitter antenna orientation (caused by fish movement) relative to the receiver antenna. Sunset and sunrise were 2121 h MDT and 0558 h MDT on the 1st observation and 1933 h MDT and 0727 h MDT on the last observation.

We used telemetry to determine home range (difference between furthest up- and downstream points) and total distance moved (sum of all observed movements) from the 1st location after implanting to the end of September (summer) and to early February (overall), and during each 24-h cycle. For these calculations we disregarded initial capture position because some fish may have been displaced during electrofishing. We also excluded fish that were followed for fewer than 50 d (n = 5). Positions ≥10 m apart were considered different.

Biweekly movement data were nonnormal (Kolmogorov-Smirnov one-sample test; $P <$ 0.001; n = 257 observations). To determine whether there were differences in movement among 2-wk intervals and between species from May to September 1994, we used 2-way Kruskal-Wallis tests. Home ranges and distances moved were analyzed by season: summer (May–September; n = 36) and overall (May–February; n = 23). Because most data also were nonnormal, differences in seasonal home ranges and distances moved between species were compared using Mann-Whitney tests. Number of positions occupied in summer was normally distributed and analyzed using t tests.

Water temperature was measured on a Ryan thermograph in the middle of the upper reach. We used daily maxima to calculate a mean maximum temperature for each 14-d period. We used rank correlation to relate mean biweekly maximum water temperature to median biweekly movement.

We compared percentage of fish active, mean signal fluctuations per minute, and mean distance moved in each 2-h period among 3 diel intervals: night, crepuscular periods (intervals containing sunset and sunrise), and day (remaining light hours). We used an arcsin transformation on the percentage of active fish. To correct for heteroscedasticity, we used a square root transformation on mean signal fluctuations per minute and mean distance moved. We examined differences between species and among times of day using 2-way analysis of variance, and we used Tukey's HSD test to compare activity at different times of day for each species. Data on diel home ranges and distances moved by each species were normal and were compared using *t* tests.

We used Biostat I, version 2.0 (Pimentel and Smith 1990), to perform the Kruskal-Wallis tests and the nonparametric Tukey's HSD tests for multiple comparisons, and SPSS/PC+, version 5.01 (SPSS 1992), for all other analyses. Throughout, we considered $P \le 0.05$ as indicating significance.

RESULTS

Biweekly observations demonstrated that brown trout moved less than rainbow trout from May to September. In summer brown trout had smaller home ranges (medians, 131 m v. 606 m; $P = 0.046$) and moved shorter distances (medians, 208 m v. 1109 m; $P = 0.018$) than rainbow trout. Brown trout also used fewer positions than rainbow trout (means, 3 v. 7; $P < 0.001$). There were no significant differences ($P > 0.89$) in the overall home range (medians, 1158 m v. 941 m) and distance moved (medians, 1971 m v. 1687 m) between brown trout and rainbow trout, which we attributed to greater mobility of brown trout from October to February, possibly associated with spawning. Nonetheless, rainbow trout had the largest summer (3865 m v. 2530 m) and overall home ranges (10,390 m v. 3452 m).

Biweekly movement of brown trout was less than rainbow trout from May to September (medians, 6 m v. 46 m; $P < 0.001$; Fig. 1). Brown trout movement peaked in late May and then declined rapidly, whereas rainbow trout were relatively active throughout the summer, with peak movement 14–27 July. Median biweekly movement of rainbow trout was positively correlated with mean biweekly maximum water temperature ($r_s = 0.80$; $P = 0.001$), though this relationship may represent a threshold response to high temperature more than a consistent trend at all temperatures. Water temperature peaked on 21, 22, and 25 July at 19.5°C. Median biweekly movement of brown trout was not related to mean biweekly maximum water temperature ($r_s = 0.26$; $P = 0.49$).

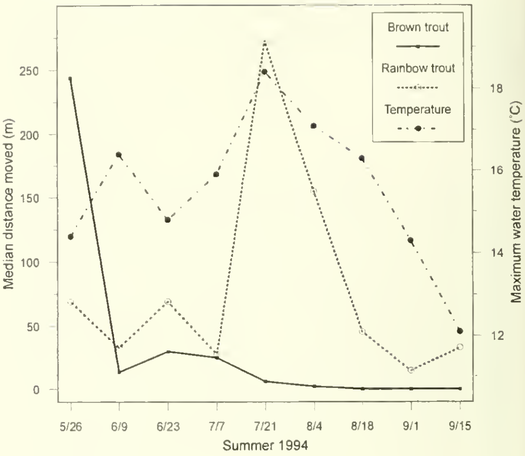

Fig. 1. Median biweekly movement of brown trout ($n = 18$) and rainbow trout ($n = 18$) from late May to late September 1994, Silver Creek, ID. Labels on the horizontal axis represent 2-wk midpoints.

Directional trends in movement were not evident. Nine of 36 trout followed in summer had moved up- and 7 had moved downstream >100 m. Eight of 22 trout followed until December or February had moved up- and 6 had moved downstream >100 m. Species differed, however, in fidelity to the site where first located. By September and by late winter, >60% of brown trout were found within 100 m of their first location. By September, <40% of rainbow trout were within 100 m of such sites, and by late winter, only 3 of 14 fish were. Such patterns suggest that brown trout use the same sites during the day throughout much of the year, whereas rainbow trout are less likely to use the same position consistently.

There were differences in diel activity between species. Throughout the diel cycle, rainbow trout had more signal fluctuations per minute than brown trout (means, 5 v. 4; $P = 0.003$), and a greater percentage of fish were active during 2-h observations (means, 87% v. 51%; $P < 0.001$). Furthermore, we observed contrasting behavior between species at different times (Table 1, Fig. 2). For brown trout the peaks in percentage of fish active and signal fluctuations per minute were at night; for rainbow trout these values were highest during the day and crepuscular periods. Whereas brown trout moved most during crepuscular periods and night, rainbow trout failed to demonstrate a significant diel pattern for this variable. There were no significant species differences ($P > 0.13$) in diel home range (means, 77 m v. 105 m) or diel distance moved (means, 192 m v. 274 m). Maximum diel home range for brown trout was 238 m and 352 m for rainbow trout.

Diel movements of brown trout were more predictable than those of rainbow trout. Brown trout left daytime locations each evening, and 8 of 10 returned before 0800 h the next day. In contrast, rainbow trout patrolled diel home ranges irregularly, often visiting the same positions throughout the 24-h cycle.

DISCUSSION

Home ranges of brown trout in Silver Creek were larger than in many other studies (Mense 1975, Bachman 1984, Hesthagen 1988), but differences may be attributed to differences in methods; i.e., tagging and mark-recapture techniques ignore behavior of marked fish that are not recaptured and tend to produce smaller home range estimates than radiotelemetry (Young 1994, Gowan and Fausch 1996). Yet the maximum home range of brown trout in Silver Creek was smaller than that of brown trout in other radiotelemetry studies (29 km, Hudson 1993; 34 km, Meyers et al. 1992; 96 km, Young 1994). Unlike those studies, we did not examine all downstream portions of Silver Creek, nor did we follow fish throughout an annual cycle; either factor could explain home range differences. Nevertheless, variables such as a greater food supply or environmental stability (e.g., reduced discharge variation or water temperature) may have rendered movement less advantageous than in other systems.

Feeding strategy and fish size may also contribute to differences in movement. Based on daytime bank observations in a Pennsylvania stream, Bachman (1984) contended that brown trout had small summer home ranges (ca 4 m long) and were active during the day. But brown trout in our study moved extensively and were largely nocturnal (also see Regal 1992, Hudson 1993). The largest fish in Bachman's (1984) study (330 mm) was smaller than the smallest brown trout in our study. Though both streams are productive spring creeks, brown trout >400 mm in Silver Creek forage primarily on large invertebrates and fish (Wilkison 1996), whereas adult brown trout in the Pennsylvania stream appeared to feed largely on drift. Piscivorous brown trout may forage more successfully at night and move to new habitats when prey become locally depleted or have fled to cover (Clapp et al. 1990). Drift-feeding juvenile brown trout in a New Zealand stream, however, were most active at night, perhaps in response to a nocturnal increase in macroinvertebrate drift (McIntosh and Townsend 1995).

TABLE 1. Activity patterns of brown trout and rainbow trout in Silver Creek, ID, May 1994 to February 1995, during the day ($n = 48$), crepuscular periods ($n = 16$), and night ($n = 32$) using means (standard deviations in parentheses) of untransformed variables. An asterisk (*) indicates a significant difference for the species main effect. For comparisons between different times of day for individual species, values followed by the same letter are not significantly different.

	Time of day		
Species	Day	Crepuscular	Night
Mean percentage of fish active*			
Brown trout	$27(32)^{a}$	$60(43)^{ab}$	$83(32)^{b}$
Rainbow trout	$98(10)^{a}$	$92(15)^{ab}$	$69(35)^{b}$
Mean fluctuations · min^{-1}*			
Brown trout	$1(1)^{a}$	$2(2)^{a}$	$8(7)^{b}$
Rainbow trout	$5(2)^{a}$	$6(3)^{a}$	$3(3)^{b}$
Mean distance moved (m) · 2 h^{-1}			
Brown trout	$6(12)^{a}$	$56(73)^{b}$	$46(58)^{b}$
Rainbow trout	$15(13)^{a}$	$30(38)^{a}$	$12(6)^{a}$

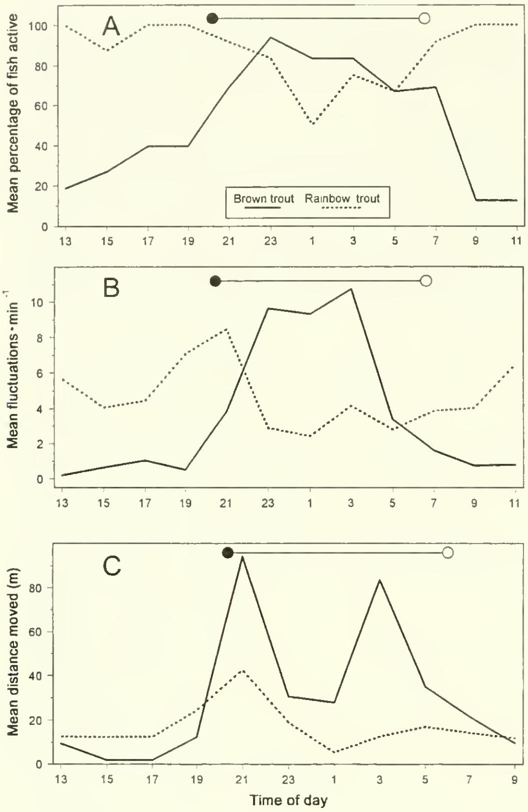

Fig. 2. Diel patterns of the (A) mean percentage of fish active; (B) mean signal fluctuations per min; and (C) mean distance moved per 2 h by species in Silver Creek, ID, on 22 June, 12 July, 17 August, and 23 September 1994 (n = 264 observations). Closed and open circles represent "average" times of sunset and sunrise, respectively. Note the change in the scale of the horizontal axis in C. Labels on the horizontal axis represent 2-h midpoints.

Rainbow trout in streams are assumed to feed primarily on drift (Elliott 1973, Tippets and Moyle 1978, Cada et al. 1987) and thus are unlikely to locally overexploit their prey. Stefanich (1952) also concluded that rainbow trout seemed more mobile than brown trout in a Montana stream. And unlike brown trout in this study and others (e.g., Clapp et al. 1990), rainbow trout showed little fidelity to daytime positions. Relative differences in movement in different streams may be related to stream size. For example, movements of rainbow trout in Silver Creek exceeded those of rainbow trout in a smaller Minnesota stream (Cargill 1980) but were less than those of rainbow trout in the larger Middle Fork Salmon River (Bjornn and Mallet 1964). Similarly, Young (1996) noted that Colorado River cutthroat trout isolated above a barrier moved less than fish in a larger connected stream segment below the barrier.

Different patterns of biweekly movement by each species were puzzling. We considered it unlikely that the early peak in brown trout activity was related to disturbance associated with electrofishing and surgery. Only 11 of 20 brown trout were implanted in mid-May. We implanted the remainder in mid-June, and the biweekly movement of this group in late June was less (median, 16 m) than that of brown trout implanted in May (median, 34 m). We speculate that brown trout movement in late May was associated with migration, possibly from outside the study area. We captured only 7 brown trout suitable for implanting during electrofishing of the lower reach of the study area in mid-May, but by mid-June large numbers of brown trout were observed and captured. Perhaps the fish captured in May were migrating to suitable summer positions, whereas brown trout captured in June had already selected such positions (see Bridcut and Giller [1993] for a similarly timed peak in brown trout emigration). Year-round tracking over a larger area would be necessary to test this assertion. The late July peak in rainbow trout movement may be attributed to fish moving to lower water temperatures, but we did not observe this species concentrating in particular areas. Clapp et al. (1990) and Meyers et al. (1992) attributed large-scale movements of brown trout to changes in water temperature, and Nielsen et al. (1994) noted that juvenile steelhead move to colder habitats as water temperatures increase. Rainbow trout also may have moved in response to decreases in dissolved oxygen. Summer fish kills attributable to hypoxia have been noted in several reaches of Silver Creek in previous years (Paul Todd, The Nature Conservancy, personal communication). Nonetheless, we cannot discount that variables such as food availability or macrophyte growth could have contributed to rainbow trout movement.

Adult rainbow trout tended to be most active during the day, which may reflect foraging preferences. Although rainbow trout can feed on drift at night (Jenkins 1969), evidence suggests this behavior is uncommon in summer (Edmundson et al. 1968, Campbell and Neuner 1985, Angradi and Griffith 1990, but see Matthews et al. 1994). Warner and Quinn (1995) noted that lentic rainbow trout moved less at night and remained inactive for long periods. Another drift-feeding species, Colorado River cutthroat trout, was consistently active only before dusk and after dawn (Young et al. in press).

In part, differences in the activity of brown trout and rainbow trout may have led to differences in summer home range and biweekly movement. Disturbed rainbow trout tended to move up- or downstream but did not seek cover. During electrofishing we observed schools of rainbow trout fleeing downstream, and we often chased them for >100 m. Because rainbow trout were active during the day, we believe that anglers frequently displaced these fish. But because brown trout often were concealed in cover during the day (see also Clapp et al. 1990, Young 1995), they were less likely to be disturbed by anglers, and those we monitored typically sought nearby cover when displaced. Lack of significant diel trends in rainbow trout movement, despite the customary trend in angler presence, suggests that angler disturbance explains only part of the difference between the 2 species. Factors such as site-specific variability in macroinvertebrate drift, inherent behavioral differences, or competitive displacement by brown trout (Gatz et al. 1987) also contribute to the greater movement by rainbow trout in summer.

Because of the growing use of radiotelemetry (Clapp et al. 1990), intensive electrofishing (Decker and Erman 1992), and 2-way fish traps (Riley et al. 1992), the prevalence of movement in stream-dwelling trout has begun to receive greater recognition. Use of radiotelemetry has enhanced the estimation of home range size and the distance that fish move, but inadequate temporal sampling may still overlook certain fish movements. For example, a 576-mm brown trout was observed in the same daytime position from 12 June 1994 to 10 February 1995; thus it had an overall daytime home range of zero. But on 3 occasions it had diel home ranges of 31 m, 121 m, and 141 m, respectively. Furthermore, median summer and mean diel home ranges (131 m v. 105 m) and distances moved (208 m v. 274 m) for brown trout were similar. These results highlight the importance of diel monitoring in evaluations of movement by stream fishes.

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SHOREBIRD PREDATION ON BENTHIC MACROINVERTEBRATES IN AN IRRIGATION RESERVOIR

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ABSTRACT.—American Falls Reservoir in southeastern Idaho is an irrigation reservoir used as an inland feeding stopover by many shorebird species. Six exclosure experiments were conducted during the 1990 drawdown period to investigate shorebird predation impact on benthic macroinvertebrate populations. The study sites differed in sediment composition, sediment slope, invertebrate densities, and shorebird abundance. Shorebird predation significantly affected invertebrate densities in only 1 of 6 experiments (Aberdeen Mouth). This site had higher sediment slope and slower water recedence than other study sites, resulting in concentration of shorebird predation on a smaller area of newly exposed sediment. Shorebird predation had the greatest impact on medium size class chironomid larvae at Aberdeen Mouth. Our results suggest that inland sites such as American Falls Reservoir represent viable shorebird habitat and may be managed to insure consistent prey availability. Drawdown rate, sediment slope, invertebrate densities, and shorebird abundance are all important factors influencing shorebird predation. Monitoring shorebird abundance and predation impact on invertebrate densities may help in manipulating drawdown rate to provide adequate shorebird prey. Management of inland sites for shorebird use may become more important in the future as human encroachment in coastal areas continues.

Key words: benthic macroinvertebrates, exclosures, Idaho, management, predation, shorebirds.

Reliable and food-rich staging areas are essential for migrating shorebirds (Senner and Howe 1984, Myers et al. 1987, Paulson 1993). Although coastal staging areas support the largest numbers of migrating shorebirds, many inland staging areas exist and may become more important as human encroachment upon coastal areas continues (Skagen and Knopf 1993). Knowledge concerning shorebird inland use is limited compared to coastal staging areas. The focus of this study was to quantify shorebird use of food resources at a freshwater inland staging area, American Falls Reservoir, Idaho. The annual presence of >30,000 individuals and >30 species of shorebirds during fall migration has been documented at this reservoir (Taylor et al. 1992). Common probing or benthic-feeding species using the reservoir include Baird's Sandpiper (*Calidris bairdi*), Western Sandpiper (*Calidris mauri*), Long-billed Dowitcher (*Limnodromus scolopaceus*), Lesser Yellowlegs (*Tringa flavipes*), and Marbled Godwit (*Limosa fedoa*).

Exclosures are commonly used to assess shorebird predation in marine and estuarine environments (Schneider 1978, Bloom 1980, Quammen 1981, Schneider and Harrington 1981, Raffaeli and Milne 1987). In this study exclosures were used to assess experimentally the impact of shorebird predation on benthic macroinvertebrates at several American Falls Reservoir sites. Sites differed in sediment composition, sediment slope, and rate of sediment exposure. Investigating the impact of shorebird predation at different sites may help identify physical factors that influence predation.

STUDY AREA

American Falls Reservoir is an east–west oriented, shallow-depth impoundment located on the Snake River, southeastern Idaho. The reservoir is part of the Bureau of Reclamation's Minidoka project that provides irrigation water to thousands of hectares of land in southern and eastern Idaho. The Snake River enters the reservoir in the Springfield Bottoms at the northeastern end and exits through a dam at the southwestern end. Located at an elevation of 1328 m, the reservoir at full capacity is 35.4 km long, has a surface area of 23,503 ha, and has 161 km of shoreline. Annual drawdown

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typically begins in April and continues through September (Fig. 1), and is most rapid between June and late August when irrigation water demand is greatest. Several kilometers of mudflats consisting mainly of sand and silt are exposed at this time.

Six experiments were conducted at the reservoir in summer 1990 (Table 1). Study sites differ in sediment composition and sediment slope and were selected because of observed shorebird foraging activity in the area. The slope of the sediment ($\tan^{-1}$ [depth of placement (m) /distance from shoreline (m)]) ranges from 0.35° to 2.69° (Table 2). The Bronco site is on the east side of the reservoir. Two experiments were conducted at Aberdeen Bay on the west side of the reservoir: one at Back Bay at the back of the bay and the other at Aberdeen Mouth at the mouth of the bay. Willow and Silo sites are at the southern end of the reservoir, within 5 km of the dam. Two experiments were conducted at the Willow site.

METHODS

For each experiment at each site we placed treatment sets in water depth inaccessible to probing shorebirds and conducted benthic sampling the day after water had receded beyond the treatment sets. A treatment set included 1 exclosure, 1 open control, and 1 exclosure control (Quammen 1981; Fig. 2). Six treatment sets were used during each experiment. The open control was marked by 4 wooden stakes. The exclosure control, which consisted of a top and 1 side to allow shorebird access, was used to account for any influence the exclosure itself might have on shorebird predation. Exclosures consisted of 4 sides and a top. Exclosures and exclosure controls were constructed of hardware cloth (1-cm^2 mesh) stapled to wooden stakes (65 cm long). The area within each exclosure or control was 0.25 m^2.

We carried treatment sets from the water's edge and placed them underwater 8.5–37 m from the shoreline (Table 1) by pushing each set into the sediment until the bottom edge of the hardware cloth was at least 2 cm below the sediment surface. Wooden stakes of the open control were pushed down to a depth equal to the other 2 treatment types. We carried all treatment sets to the placement area from a downshore point to minimize sediment disturbance between treatments and the shoreline. The 6 treatment sets were placed in a row parallel to the shoreline in the same water depth (Fig. 2). Arrangement of the exclosure and 2 controls in each treatment set was random. Placement depth for treatment sets in each experiment ranged from 19 to 40 cm (Table 1). Reservoir drawdown was constant and averaged 14 (±3 *s*) cm/day during the study period (July to mid-August 1990). The rapid drawdown resulted in the treatment sets being submerged 1–4 d at each site (Table 1).

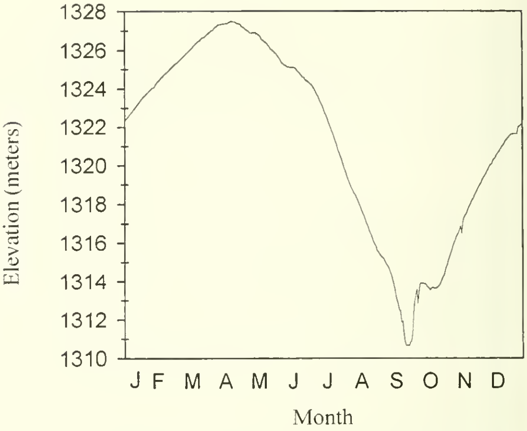

Fig. 1. Daily average water level at American Falls dam from 1 January to 31 December 1990.

Benthic macroinvertebrates were sampled the day after the water had completely receded beyond all treatment sets. Because treatment sets were placed parallel to the shoreline, all became exposed at the same time and were sampled simultaneously according to the following procedures: We took randomly spaced cores of sediment with a 5-cm-diameter, 10-cm-long plastic core tube. Two cores were taken from each exclosure and control and then combined to represent a single sample, generating 6 samples for each treatment type (exclosure, exclosure control, open control) during each experiment. Sediment cores taken in the field were placed in plastic sample bags and either sorted or frozen as soon as possible. Before sorting, we sieved samples (0.25-mm mesh sieve), leaving only invertebrates and organic matter. All invertebrates were sorted from the samples, preserved in 95% ethanol, and later identified and counted with the use of a binocular dissecting microscope. Three distinct size classes of chironomid larvae, differentiated by

TABLE 1. Summary of experimental design parameters including water depth in which treatments were placed and initial distance of treatments from shoreline.

Site name	Placement date	Sampling date	Placement depth (cm)	Distance from shore (m)
Bronco	18 July	20 July	23	37
Back Bay	26 July	28 July	40	8.5
Silo	6 August	9 August	40	30
Aberdeen Mouth	9 August	14 August	27	10
Willow (experiment 1)	14 August	16 August	19	31
Willow (experiment 2)	18 August	20 August	22	35

TABLE 2. Sediment slope and sediment composition at each study site.

Site name	Sediment slope	% silt (<.62 mm)	% sand (.62–1.6 mm)	% gravel (>1.6 mm)
Bronco	0.35	28.8	71.2	0
Back Bay	2.69	62.7	37.2	0.1
Silo	0.76	59.0	40.6	0.4
Aberdeen Mouth	1.55	96.6	3.4	0
Willow (experiment 1)	0.36	73.4	26.6	0
Willow (experiment 2)	0.36	78.2	21.8	0

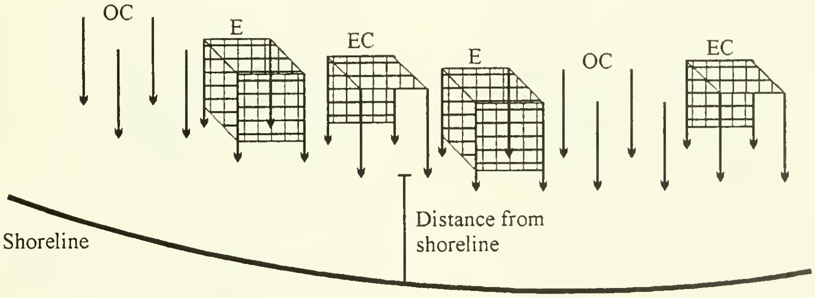

Fig. 2. Depiction of the placement of 2 treatment sets parallel to the shoreline. A treatment set consisted of 1 exclosure (E), 1 exclosure control (EC), and 1 open control (OC). Ordering of the exclosure and controls in each treatment set was random.

head capsule size and body length (small, <5 mm; medium, 5–10 mm; large, >10 mm), were counted separately. We took 1 sample from each study site and analyzed it for sediment composition. This sample was wet-sieved through 2 sieves to separate it into gravel (>1.6 mm), sand (>0.62 mm), and silt (<0.62 mm) components. After removing invertebrates, we dried the sample at 60°C for 72 h and weighed it. Percentages of gravel, sand, and silt at the study site were then calculated from the components and total weight of the sample (Table 2).

A daily estimate of shorebird abundance in the immediate vicinity of the treatment sets was calculated beginning the day after sets were placed and continuing through the day benthic sampling was conducted. Direct counts were made of all probing species in a 100-m area of shoreline in front of the treatment sets. This area was designated by 2 small flags placed at both ends of the transect. For a period of 30 min each morning, we counted all shorebirds at 5-min intervals (Wilson 1988). Counts of probing species were used to calculate a mean and standard deviation, which when doubled represented an hourly estimate. Multiplying the hourly estimate by 24 yielded a daily estimate of shorebird abundance during each experiment.

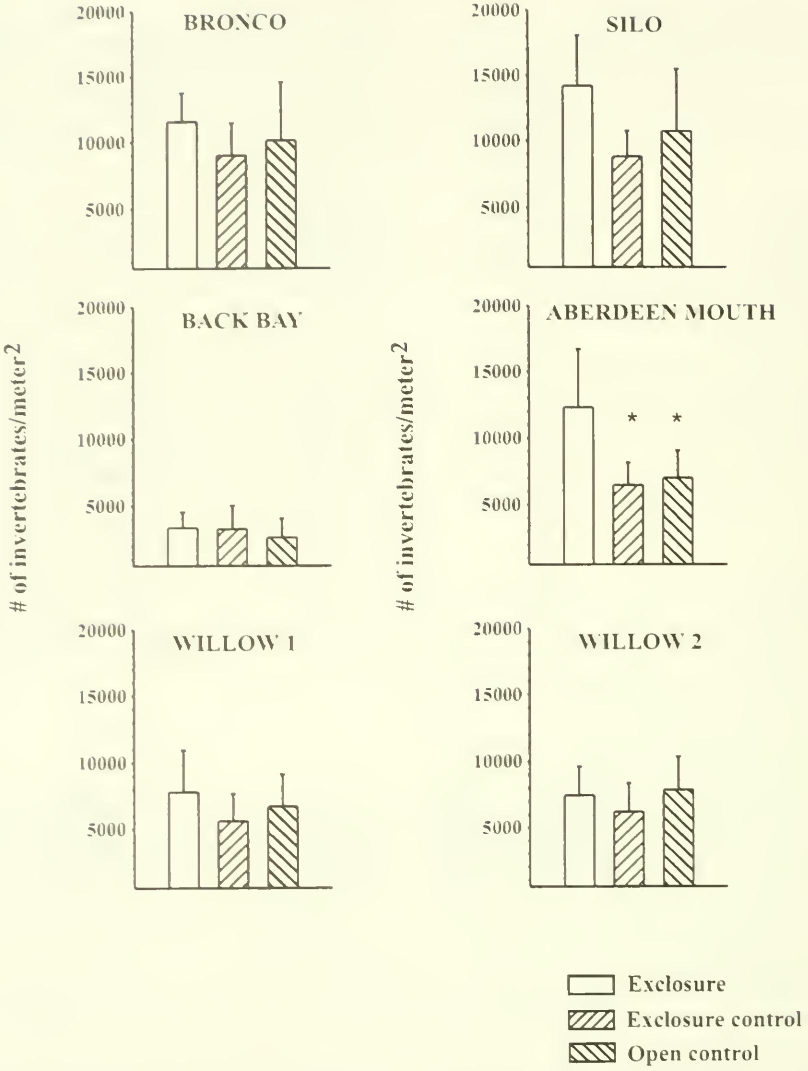

Fig. 3. Mean total invertebrate densities in exclosures and controls during each experiment. Error bars indicate 1 standard deviation from the mean. An asterisk (*) indicates a significant difference ($P < 0.05$) between total invertebrate densities in exclosures and controls.

Comparison of shorebird abundance across all study sites was possible because daily estimates were based on counts taken at a similar time at each study site.

An independent *t* test was used to compare invertebrate density data from the 2 types of controls, addressing the effect of exclosure presence on shorebird predation. An ANOVA was used to compare invertebrate density data from all 3 treatment types at each site. Total invertebrate density data were analyzed as well as large and medium size class density data for chironomid larvae. We used size class data analysis to address the possibility of shorebird feeding preference for either size class, and a linear regression to investigate the relationship between sediment composition and invertebrate densities at each site.

RESULTS

Benthic prey items available to shorebirds at American Falls Reservoir included chironomid larvae and tubificid worms. Invertebrate densities differed across study sites (Fig. 3). Most chironomid larvae consisted of *Chironomus* sp.

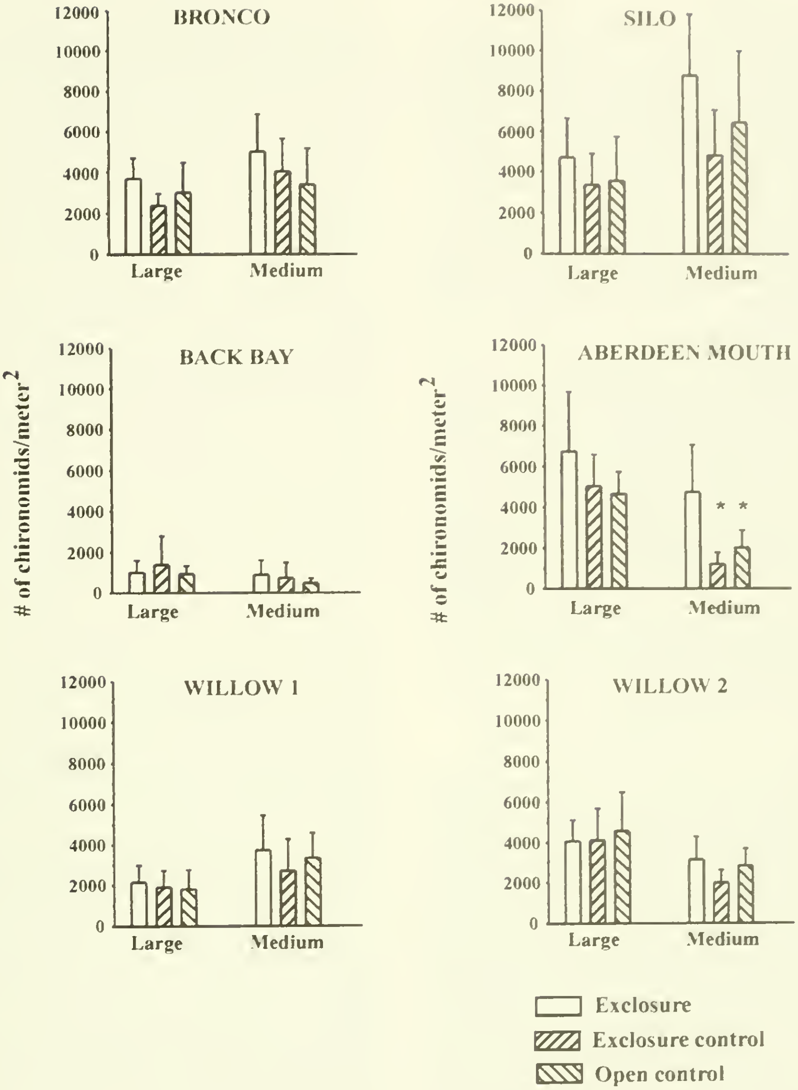

Fig. 4. Mean densities of large size class chironomid larvae and medium size class chironomid larvae in exclosures and controls during each experiment. Error bars indicate 1 standard deviation from the mean. An asterisk (*) indicates a significant difference ($P < 0.05$) between chironomid densities in exclosures and controls.

(90–95%), but some *Procladius* sp. also were found. Chironomid larvae were the predominant benthic prey item, constituting 40–100% of total benthic invertebrates found in exclosures during each experiment. The majority of chironomid larvae in samples were represented by the large and medium size classes. Individuals of these 2 size classes were 1–2 mm larger in diameter than tubificid worms. Densities of large and medium size class chironomid larvae were similar at each site but differed somewhat across sites (Fig. 4). The largest number of chironomid larvae were found at the Silo site, the smallest number at Back Bay.

No differences ($P > 0.05$) in total invertebrate densities occurred between the 2 control types in any experiments. A difference ($P < 0.05$) between total invertebrate density among the 3 treatment types occurred only during the Aberdeen Mouth experiment (Fig. 3). Comparison of chironomid size class data from the treatment types revealed a difference ($P < 0.05$) only in the medium size class of chironomids at Aberdeen Mouth (Fig. 4). The impact of shorebird predation on the large size class of chironomids at this site was noticeable but not significant ($P < 0.10$). At the Silo site the medium size class of chironomids suffered greater predation impact than the large size class, but this difference was not significant ($P < 0.10$; Fig. 4).

Sand and silt dominated all sites (Table 2). The percentage of these 2 fractions varied from site to site, but linear regression results indicated no effect of sand ($r = 0.22$, $P > 0.05$) or silt concentration ($r = -0.22$, $P > 0.05$) on benthic invertebrate densities. Because of the rapid water drawdown during the experiments, more than 10 m of sediment was exposed or under shallow water (<5 cm) each day at 4 of the 5 sites. At Aberdeen Bay where 2 experiments were conducted (Back Bay, Aberdeen Mouth), 0–5 m of sediment was exposed each day. Daily estimates of shorebird abundance varied widely, ranging from 14 during the Silo experiment to over 6000 during the Bronco experiment (Table 3).

DISCUSSION

Management of American Falls Reservoir for irrigation purposes has created a unique and dynamic environment with gradually sloping sediment, constant rate of summer drawdown, and little submerged vegetation (Taylor et al. 1993). These characteristics represent ideal habitat for foraging shorebirds during migration (Rundle and Fredrickson 1981, Kushlan 1989, Helmers 1991). Shorebird abundance data were not useful predictors of predation impact on invertebrate densities at the study sites. This may be because birds were foraging over large areas of freshly available sediment each day, and counts were taken during only 1 window of time daily. Significant shorebird predation effect on benthic prey populations was found only at Aberdeen Mouth. Shorebird predation at this site had a greater impact on medium size class chironomids (Fig. 4), suggesting a feeding preference for size class. The possibility of feeding preference should not be overlooked in management decisions concerning shorebirds. Further study of shorebird preference for prey size or species in freshwater environments is needed.

Comparing conditions at the Aberdeen Mouth site to those at other study sites was useful in identifying factors that influenced shorebird predation impact during this study. At Aberdeen Mouth, treatment sets were exposed to shorebird predation at least 24 h longer than at other sites because the mouth of the small bay has a steeper sediment slope than all other sites except Back Bay. The combination of steeper slope and drainage of water from the bay resulted in slower water recedence. Shorebird predation at the Aberdeen Mouth site was concentrated on 0–2 m of freshly exposed sediment each day rather than 5–10 m of freshly exposed sediment typical of the other study sites. The longer exposure and concentration of shorebird predation on a smaller area of sediment probably accounts for the observed impact on invertebrate densities at the Aberdeen Mouth site. Although sediment slope was steepest at the Back Bay site (Table 2), the minimal impact of shorebird predation was probably due to much lower invertebrate densities (Fig. 3) and shorebird abundance (Table 3) compared to the other study sites. Our results suggest that sediment slope, invertebrate densities, and shorebird abundance should all be monitored and considered in combination when making management decisions regarding shorebird predation.

Conditions at American Falls Reservoir are a contrast to conditions in coastal areas. The

TABLE 3. Daily abundance estimates (mean ± standard deviation) of shorebirds during each experiment. Numbers of counts reflect different lengths of each experiment.

Site name	Day 1	Day 2	Day 3	Day 4
Bronco	6034 ± 1482	630 ± 199*		
Back Bay	15 ± 1	60 ± 44*		
Silo	14 ± 36	240 ± 40	41 ± 109*	
Aberdeen Mouth	1008 ± 469	254 ± 151	117 ± 67	103 ± 81*
Willow (experiment 1)	3408 ± 1761	2722 ± 511*		
Willow (experiment 2)	199 ± 216*			

* = last day surveyed

latter are characterized by many shorebirds feeding on a limited shoreline exposed during low tide (Myers 1983, Burger 1984). Coastal studies have documented a significant impact of shorebird predation on invertebrate densities (Schneider 1978, Schneider and Harrington 1981, Quammen 1984). At American Falls Reservoir the constant summer drawdown rate provides large areas of newly exposed sediment daily, and shorebird densities are lower than at coastal areas. Our results suggest that current prey densities in both sandy and silty mudflats are adequate to support shorebirds using American Falls Reservoir. This potential is encouraging because if shorebird densities were to increase, use of the traditional feeding areas might gradually increase over time (Myers et al. 1987). Although further study of inland sites is needed, conservation and management of these sites should continue.

Our results and those of other studies have identified criteria for evaluating inland areas as potential shorebird staging areas. Impoundments currently used for irrigation purposes may need only minor adjustments to accommodate migrating shorebirds. A gradually sloping, silty or sandy sediment with little or no vegetation is most favorable (Helmers 1991). An annual drawdown would favor prey colonization by tubificid worms and certain chironomid species and discourage colonization by aquatic vegetation (Helmers 1991). The drop in water level must coincide with known migration periods of shorebird species that would potentially use the area (Hands et al. 1991, Taylor et al. 1993). A gradual but continual drop in water level would insure a renewing source of available prey (Rundle and Fredrickson 1981, Kushlan 1989). Prey densities will likely vary across space and time and should be monitored throughout the migration period. Ability to manipulate the drawdown rate on a seasonal or yearly basis is important. Faster drawdown may be necessary to compensate for sediment slope in some impoundments. The drawdown rate may also be manipulated to accommodate numbers of shorebirds using the area in relation to densities of available prey. Monitoring the impact of shorebird predation on invertebrate populations could be accomplished using exclosures, thus providing data for decisions concerning drawdown rate (Skagen and Knopf 1993).

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LAGOMORPHS AND THE DISPERSAL OF SEEDS INTO COMMUNITIES DOMINATED BY EXOTIC ANNUAL WEEDS

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ABSTRACT.—Large areas of western rangeland are presently dominated by alien annual weeds such as *Bromus tectorum* (cheatgrass). These communities resist succession to perennial communities primarily because the annuals are competitively superior to establishing perennial seedlings and they promote fires that favor weeds over perennials. Succession may be further slowed, however, by low rates of seed dispersal into annual grasslands. We investigated the role of lagomorphs (*Sylvilagus nuttallii*, Nuttall's cottontail; *S. audubonii*, desert cottontail; and *Lepus californicus*, black-tailed jackrabbit) in seed dispersal across an ecotone between an open juniper woodland and an annual grassland. We collected pellets along five 100 × 2-m transects parallel to the ecotone: 50 m into woodland, border, and 20 m, 50 m, and 100 m into grassland. We searched pellets for juniper seeds visually and for any other species through germination from crushed pellets after cold, moist stratification. Pellets were not evenly distributed across transects, but there was no trend with respect to position of transect. *Juniperus osteosperma* (Utah juniper) was the most abundant seed. Both the number of juniper seeds and the proportion of pellets with juniper seeds decreased steadily from a high in woodland to absence at 100 m into grassland. Only 2 dicot seedlings emerged from pellets, 1 *Salsola pestifer* and 1 unknown that died prior to identification. Consequently, there was little seed movement into the grassland; 72% of all seeds were collected from either woodland or border transects. Lagomorphs apparently do not effectively replenish the native perennial seed pool of cheatgrass-dominated disturbances at Dugway.

Key words: Juniperus osteosperma, *seed dispersal, lagomorphs,* Bromus tectorum, *range restoration, degraded rangeland.*

Overgrazing, fires, and other disturbances from human activities have degraded extensive areas of native vegetation in the Intermountain region of the western USA, leading to the domination of many rangelands by alien annual weeds such as *Bromus tectorum* (cheatgrass), *Taeniatherum asperum* (medusahead), and *Salsola pestifer* (Russian thistle; Billings 1990, Young 1994). Over 1.3 million ha are completely dominated by *B. tectorum* or *T. asperum* and 30.8 million ha more are infested or susceptible to invasion (Pellant and Hall 1994). Once established, these annual grasslands largely resist succession to native rangelands because the weeds are highly competitive with establishing perennials (Monsen 1994, Pyke and Novak 1994, Young 1994), and because of the initiation of a "cheatgrass-wildfire" cycle wherein annual weeds promote fire that favors the further spread of weeds and thus of more fires (Billings 1990, Whisenant 1990, Peters and Bunting 1994).

Although competition and increased fire frequencies make it difficult for native species to reestablish, given enough time between fires at least some native species such as *Sitanion hystrix* (bottlebrush squirreltail; Hironaka and Sindelar 1973) and *Agropyron smithii* (western wheatgrass; Monsen 1994) appear able to invade these weed communities. In addition to competition and repeated fires, then, succession to native perennial rangelands may be partly limited by low seed availability due to depletion of the native seed bank over time (Pyke 1994, L.D. Humphrey and E.W. Schupp unpublished data) and potentially low levels of dispersal into the annual grasslands.

Lagomorphs, however, may effectively disperse seeds from native rangelands into annual grasslands. They range widely, feeding in shrubland, woodland, and grassland (Smith 1948, Kundaeli and Reynolds 1972, Westoby and Wagner 1973, McAdoo et al. 1987, Zeveloff 1988, Smith 1990) and, in the process, disperse viable

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seeds (1) of grasses and forbs consumed incidentally while feeding on foliage (Welch 1985, Zedler and Black 1992, Malo and Suárez 1995, Malo et al. 1995) and (2) of fleshy-fruited plants whose fruits are intentionally consumed (Smith 1948, D'Antonio 1990, Schupp et. al 1996, 1997).

The objective of this study was to examine the role of lagomorphs in the dispersal of seeds across an ecotone between a relict open juniper woodland and a burned area dominated by exotic annual weeds. We were especially concerned with (1) the diversity and quantity of native and exotic seeds found in pellets and (2) the spatial pattern of native seed deposition in the grassland relative to distance from the woodland.

STUDY SITE

The study site is an open juniper woodland and adjacent annual grassland on the U.S. Army Dugway Proving Grounds, Tooele County, Utah, USA (≈40°15′N, 112°50′W), at an elevation of ≈1460 m, roughly where old Lake Bonneville sand dunes meet the lower slopes of the Cedar Mountains. The climate is arid, with mean annual precipitation of 19.2 cm (Bagley 1991). Aerial photographs show that wildfire converted a shrubland adjacent to the woodland into an annual grassland sometime between 1978 and 1985 (R. Johnson personal communication). The burn was seeded with *Agropyron cristatum/A. desertorum* (crested wheatgrass) and *Kochia prostrata* (prostrate kochia) after the fire, but the seeding was not very successful and densities of these exotic perennials are low. Native perennials such as the grasses *Oryzopsis hymenoides* (Indian ricegrass) and *Sporobolus cryptandrus* (sand dropseed) and the forbs *Sphaeralcea munroana* (Munroe's globemallow) and *Oenothera pallida* (pale evening primrose) are also present at low densities. The overwhelmingly dominant species, however, are exotic annual weeds, mostly *B. tectorum* with variable quantities of *S. pestifer* and *Sisymbrium altissimum* (tumbling mustard).

Vegetation within the adjacent woodland consists of scattered large *Juniperus osteosperma* (Utah juniper) with a well-developed shrub understory of predominantly *Atriplex canescens* (four-wing saltbush) and *Sarcobatus vermiculatus* (greasewood), and a diverse herbaceous layer including *Erysimum asperum* (wallflower), *Eriogonum* spp. (buckwheats), and the native perennials listed from the burn. All annual weeds from the burn are also found in low densities scattered through the adjacent woodland. The lagomorphs *Sylvilagus nuttallii* (Nuttall's cottontail), *S. audubonii* (desert cottontail), and *Lepus californicus* (black-tailed jackrabbit) are present at the site.

METHODS

In February 1995 we placed a transect 100 m long × 2 m wide in the annual grassland directly adjacent to the border of the juniper woodland (transect = 0), successive transects at 20 m (+20), 50 m (+50), and 100 m (+100) into the grassland, and a final transect 50 m into the woodland (–50). All transects were parallel to the border. After clearing *S. pestifer* skeletons with a pitchfork, we collected all intact lagomorph feces (pellets) encountered in each transect. After completing collections, we realized that we had used a more thorough technique on the +100 m transect, pulling up cheatgrass to expose pellets trapped within clumps of vegetation or within the upper few cm of soil. Consequently, we re-collected remaining transects with the same thoroughness.

Decomposition of lagomorph pellets in arid environments is slow. In west Texas, Flinders and Crawford (1977) estimated time for complete decomposition to be 4.4 yr for *L. californicus* pellets and 9.5 yr for *S. audubonii* pellets. Consequently, these collections represent long-term patterns of deposition, suggesting the results are, at least for this single site, relatively robust. Accumulations are not so long term, however, that collections from the annual grassland (≥10 yr old) would be biased by inclusion of significant numbers of relict pellets deposited in the former shrubland.

Pellets were kept in plastic bags in a refrigerator until processing. Because larger pellets are more likely to contain seeds than small pellets (E.W. Schupp, M. Fuentes, and J.M. Gómez unpublished data), we randomly selected 25 pellets/transect and measured length to the nearest 0.1 mm with dial calipers to compare pellet size across transects. We then processed the entire sample from each transect by cleaning the surface of each pellet with a stiff camel hair brush to dislodge any seeds clinging to the surface and then crushing all pellets to search for the relatively large and obvious seeds of juniper and the shrubs. We did not open juniper seeds to determine percent filled because the only cone crop available for dispersal in the 2 yr preceding this study had <1% filled seeds when mature (E.W. Schupp unpublished data). Because lagomorphs do not appear to discriminate among cones based on seed filling (E.W. Schupp, M. Fuentes, and J.M. Gómez unpublished data), results should also be representative of years with high levels of filled seeds.

Due to the difficulty of locating small seeds in fibrous remains of pellets, we searched for the presence of species other than juniper with germination tests. After breaking pellets apart further, we spread them on wet washed sand in 0.25 × 0.50-m plastic nursery trays, wet the pellet materials, covered them with plastic lids to prevent drying, and placed them in a refrigerator at ≈3–4°C from 16 June to 28 August 1995 (73 d). On 28 August we placed the trays in a growth chamber with a 24-h cycle of 12 h light at 15°C and 12 h dark at 10°C. After 5 wk we increased temperatures to 20°C and 15°C, respectively, but terminated the experiment after 3 d because temperature began fluctuating wildly. While the experiment was in progress, we misted pellet material daily and transplanted emerging seedlings to small pots to grow until identified.

We used chi-square goodness of fit tests to analyze distributions of pellets and seeds across transects with an expectation that they would be evenly distributed, and a likelihood ratio chi-square test of a 2 × 5 contingency table to analyze for differences among transects in proportions of pellets with and without seeds. Spearman rank correlations tested for trends in number of pellets, number of seeds, and proportions of pellets with seeds as functions of distance from the woodland transect. We analyzed differences among transects in pellet size (length) with one-way ANOVA followed by a Tukey HSD post-hoc test to determine which transects differed; because a normal probability plot suggested the data were normally distributed and a Bartlett's test ($\chi^2_{[4]} = 6.122$, $P = 0.190$) demonstrated homogeneity of group variances, we used untransformed data. Analyses were performed with SYSTAT 5.0 (Wilkinson 1990).

RESULTS

We collected a total of 8425 pellets from the 1000 m^2 sampled. Pellets were not evenly distributed across transects ($\chi^2_{[4]} = 797.97$, $P \ll 0.0001$). There was, however, no relationship between number of pellets and distance from the woodland transect ($r_s = 0.200$, $n = 5$, $P > 0.5$). The greatest number of pellets was found at +20 m, and the least at +100 m (Table 1).

Pellet size, as measured by length, differed significantly among transects ($F_{[4,120]} = 11.8$, $P < 0.001$). The difference was due entirely to the –50 transect having larger pellets than all other transects, which did not differ from each other (Table 1).

Fifty-seven pellets (0.7%) contained a total of 61 whole and apparently undamaged juniper seeds; 1 contained 3 seeds, 2 contained 2 seeds, and the remainder contained a single seed. An additional 17 pellets contained broken seeds or seeds separated along the seam joining the 2 halves of the seed coat. No other large-

TABLE 1. Number of pellets, mean pellet length (mm), number of pellets with whole seeds, proportion of pellets with whole seeds, and number of whole seeds by transect. For pellet length, values followed by the same letter are not significantly different at $P < 0.05$ based on a Tukey HSD test.

	Pellets				
Transect	Number	Length [mean (*s*)]	Number with seeds	Proportion with seeds	Number of seeds
WOODLAND					
–50	1588	11.1 (1.3) a	25	0.0157	28
ECOTONE					
0	1436	9.8 (1.4) b	16	0.0111	16
GRASSLAND					
+20	2597	9.5 (1.1) b	11	0.0042	12
+50	1777	9.0 (0.9) b	5	0.0028	5
+100	1027	9.7 (1.0) b	0	0.0000	0

seeded species were found in the pellets. Considering only whole seeds, a 2 × 5 contingency table analysis showed the proportion of pellets containing seeds differed among transects (likelihood ratio $\chi^2_{[4]} = 38.44$, $P < 0.001$; Table 1). Similarly, a chi-square analysis showed that numbers of whole seeds were not evenly distributed across transects ($\chi^2_{[4]} = 38.10$, $P < 0.001$; Table 1). In contrast to the number of pellets, both the proportion of pellets with seeds and the number of seeds decreased steadily with increasing distance from the woodland ($r_s = -1.00$, $n = 5$, $P = 0.05$ in both cases; Table 1). Analyses using all seeds (whole + broken) yielded virtually identical results.

Only 2 seedlings emerged from the rabbit pellet fragments during germination tests. After 7 d 1 *S. pestifer* emerged from the +20 transect material and after 35 d 1 unidentified dicot emerged from the +100 transect material but died before growing to an identifiable size.

DISCUSSION

Although the lack of replication across sites makes it difficult to generalize results beyond our site, the fact that our samples represent relatively long-term accumulations of pellets strengthens interpretations for this site. Our results strongly suggest that lagomorphs do not effectively disperse seeds of native species into weed-infested communities at Dugway. Consequently, they appear to contribute little to replenishing the native seed bank in these degraded areas.

Though not abundant, the most frequently encountered seed was that of juniper. This supports the growing realization that lagomorphs are involved in seed dispersal of fleshy-fruited species in general (D'Antonio 1990, Nogales et al. 1995), and of junipers in particular. They have been recorded dispersing *J. pinchoti* and *J. ashei* in Texas and Oklahoma (Smith 1948), *J. osteosperma* in Utah (this study, Schupp et. al 1996), *J. occidentalis* in Oregon (Schupp et al. 1997), and *J. phoenicea* in southwestern Spain (Muñoz-Reinoso 1993). Although the European rabbit (*Oryctolagus cuniculus*) breaks many juniper seeds (Muñoz-Reinoso 1993), the large number of damaged seeds in this study was not found in Oregon (Schupp et al. 1997) or at 2 other Dugway sites only a few km from the present site (Schupp et al. 1996). Many of these broken seeds were apparently old unfilled ones beginning to split along the seam after several years in a pellet.

The percentage of pellets with juniper seeds in this study was considerably lower than the 4–7% reported for the 2 nearby woodland sites (Schupp et al. 1996). This is probably a function of irregular fruiting of *J. osteosperma*; while pellet collections for the previous study corresponded to a period of heavy fruitfall, the present study includes pellets deposited over many years, encompassing years with both heavy and light fruit production. Even if more seeds were dispersed, however, few would be dispersed much beyond the boundary of the woodland; 72% of all seeds were found in either the woodland transect or directly along the border, and the number of seeds dropped off rapidly to zero at 100 m.

Reasons for this pattern of dispersal are uncertain. Based on pellet counts, *L. californicus* use of seeded grasslands has been documented to decrease with distance from native shrubland, although in 2 of 3 sites the decrease was not evident within the 100-m range we consider in this study (Westoby and Wagner 1973, McAdoo et al. 1987). Similarly, numbers of pellets, and thus presumably activity, did not decrease with distance from woodland in this study—overall decreased lagomorph activity with distance cannot alone explain the detected pattern of juniper seed deposition. Variation in pellet size also cannot fully explain the pattern. Larger pellets are more likely to contain juniper seeds (E.W. Schupp, M. Fuentes, and J.M. Gómez unpublished data) and pellets were larger in the woodland, but pellet size did not change from 0 to +100 while the number of juniper seeds dropped rapidly. It is possible that the lagomorph species differ in both the importance of juniper in the diet and in habitat use such that the species dispersing the most juniper seeds is (are) also least likely to forage out into the grassland. We have no data on abundances of the 3 species nor species-specific data on either juniper feeding or foraging location, but known differences between *Sylvilagus* spp. and *L. californicus* in habitat preference and predator-escape strategies (Zeveloff 1988) suggest *Sylvilagus* spp. might be less likely to venture into the grassland. If they also disperse more juniper seeds than *L. californicus*, the pattern of dispersal is easily explained. Since *L. californicus* is a larger species, however, it should produce the larger pellets. If so, the distribution of pellet size across transects and the generally greater occurrence of seeds in larger pellets argue that it is in fact *L. californicus* that is least likely to forage away from the woodland and most likely to disperse juniper seeds. Although this is contrary to expectations based on habitat affinities, it could explain the pattern of dispersal. A final possible explanation is that gut passage is rapid relative to the rate at which lagomorphs move out into the grassland, and that although they continue to move and feed, they void most juniper seeds near the woodland. No data exist for evaluating this possibility.

We were especially surprised by the low number and diversity of other species in pellets. In southern California, Zedler and Black (1992) germinated 10 herbaceous species from *Sylvilagus* spp. pellets at a rate of ≈87 seedlings per 1000 pellets. In central Spain, Malo and Suárez (1995) germinated 2034 seeds of 52 herbaceous species from 312 g of *O. cuniculus* pellets, equivalent to ≈2200 of our pellets. More similar to our results, Welch (1985) found fairly low levels of emergence of 8 species from hare (*Lepus europaeus* and *L. timidus*) and rabbit (*O. cuniculus*) pellets in Scotland. Part of the difference is likely due to methods. Other studies used repeated collections of fresh pellets (up to several months old), while ours was a single collection of pellets spanning at least several years of age; repeated collections of newly deposited pellets may have yielded greater numbers of emerging seedlings at our site. Additionally, our germination experiments ended after 38 d. Nonetheless, the nearly total lack of seedling emergence from 8425 pellets is striking; lagomorph dispersal of herbaceous species at Dugway is apparently an unusual event.

One last observation is worth noting. The peak in pellet density at +20 was associated with 2 relict shrubs, 1 on and the other adjacent to the transect. Pellets were extremely abundant in the vicinity of these shrubs, which is compatible with the notion that jackrabbit activity in open habitats is concentrated in the vicinity of protective shrubs (Longland 1991). In other systems where lagomorphs may be more important in dispersing seeds of native species, their use in restoration of open grassland may be enhanced by first planting scattered shrubs throughout the grassland to provide cover from predators. These shrubs may then become foci for lagomorph-mediated invasion of native species.

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PSEUDOCROSSIDIUM OBTUSULUM (POTTIACEAE, BRYOPSIDA) NEW TO MONTANA WITH A KEY TO NORTH AMERICAN SPECIES IN THE GENUS

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ABSTRACT.—The moss species *Pseudocrossidium obtusulum* (Lindb.) Crum & Anderson is reported for the state of Montana. Recent systematics of the genus *Pseudocrossidium* in North America is discussed.

Key words: mosses, bryophytes, Montana, Pseudocrossidium, P. crinitum, P. hornschuchianum, P. obtusulum, P. replicatum, P. revolutum.

Montana has one of the richest recorded moss floras of the western United States, with 410 known species and varieties (Elliott in preparation). Although most collecting has occurred in the western portion of the state, a concentrated examination of particularly dry habitats in Ravalli County has yielded species new to the state (Eckel, Hoy, and Elliott in preparation). These species are members of a cryptoflora of minute bryophytes occurring on various soil substrates, of which one is the following species:

Pseudocrossidium obtusulum
(Lindb.) Crum & Anderson

USA, Montana, Ravalli Co., east side of Bitterroot Valley, North Birch Creek watershed: 7 miles SSE of Stevensville, NW NE Sec. 12, T7N, R19W, 3600′ elev., from vertical S-facing cliff face, N side of irrigation ditch just above old water level; *Hoy 306*, April 6, 1996 (BUF).

There are 5 species of *Pseudocrossidium* Williams presently listed in the moss flora of North America north of Mexico (Anderson et al. 1990). Spence (1987) has given a good review of the literature and American distribution of 4 of these, the 5th being *P. obtusulum* (Lindb.) Crum & Anderson, a species considered by some to be a variety of *P. revolutum* (Brid. in Schrad.) Zand. (Tan et al. 1981), and by others to be indistinguishable from the latter in local populations in the field (McIntosh 1986). The variety was elevated to species status by Crum and Anderson (1989) for the North American checklist (Anderson et al. 1990), but without discussion. Zander (manuscript in preparation) has determined that *P. revolutum* does not occur in the Arctic or Greenland, or elsewhere in North America. Because one of the obstacles to the convenient study of arid bryophyte cryptofloras is the scattered taxonomic treatments, an attempt has been made here to summarize the genus to date in North America with a key and illustrations to the 5 species.

Historically, species in the genus *Pseudocrossidium* have been placed in the genera *Barbula* Hedw., *Desmatodon* Brid., and *Tortula* Hedw. However, most are distinguishable from these genera by the strongly and strikingly revolute leaf margins, most evident on transverse sections of the leaf, resembling 2 cylinders separated by a groove (Zander personal communication) as opposed to the usual plain or narrowly recurved leaves of other species of other genera. The character of differentiated perichaetial leaves may differentiate the genus in the broadest sense, especially species in South America where the bulk of the species occur; but for the 4 taxa occurring in North America (here excluding *P. revolutum*), only *P. hornshuchianum* has such—a species found to date in North America in only 2 botanical gardens, 1 in British Columbia (Tan et al. 1981), the other in Massachusetts (Mishler and Miller 1983).

The genus is separated from *Barbula* and other genera of the Barbuloideae, such as *Didymodon*, by the absence of a ventral stereid

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band in the costa. Neither *Desmatodon* nor *Tortula* has this feature either, or it is occasionally weakly present. McIntosh (1986) has also pointed out the useful character of the sharp and deep costal groove or keeled leaf in *Pseudocrossidium*, whereas in *Tortula* and *Desmatodon* the leaf is broadly channeled and the costa in section is nearly circular with an elevation, sometimes distinctive, on the ventral surface composed of differentiated cells. Zander (1993) has indicated that the crescent-shaped dorsal stereid band, as opposed to the semicircular band of *Desmatodon* and *Tortula*, is distinctive in *Pseudocrossidium*.

McIntosh (1986) has also distinguished *P. obtusulum* (as *P. revolutum*) from *Didymodon brachyphyllus* (Sull. in Whippl.) Zand., a species sometimes associated with *P. obtusulum*, by the dense papillae, as well as the lack of ventral stereid band. *Tortula muralis* Hedw. and its closely related if not synonymous species, *Tortula brevipes* (Lesq.) Broth. and *Desmatodon plithobius* Sull. & Lesq., also have broadly spirally once-revolute margins and densely papillose leaves, but usually have a rather long, smooth awn. Tiny specimens may, however, be only mucronate and are distinguished from *P. obtusulum* by the latter's flattened, crescent-shaped dorsal stereid band.

Key to *Pseudocrossidium* Species in North America and Greenland

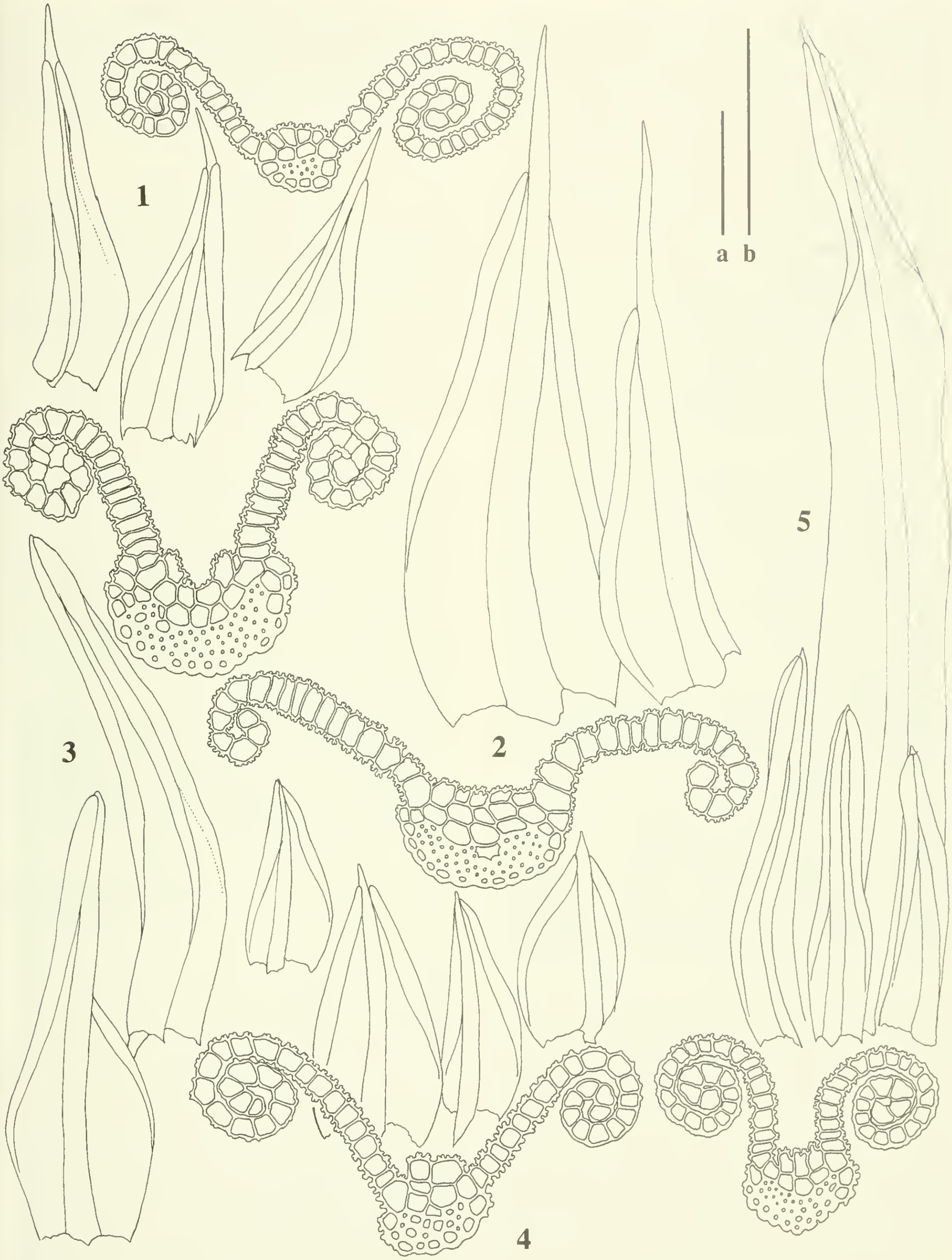
(Figs. 1–5)

1. Leaves short- to long-awned:
    2. Leaves rounded-obtuse at base of long awn; ventral costal surface concave; guide cells 4; Mexico, Arizona, New Mexico, Texas, Utah . . . . *Pseudocrossidium crinitum* (= *P. aureum*)
    2. Leaves acute at base of short-awn; ventral costal surface convex; guide cells 2; botanic gardens in British Columbia and Massachusetts . . . . *Pseudocrossidium hornschuchianum*
1. Leaves merely apiculate to short-mucronate:
    3. Leaves relatively long, 1.0–1.5 mm, ligulate to oblong-lanceolate, apex obtuse; ventral costal surface concave; guide cells (4–) 6; margins strongly spirally revolute, inrolled margins of bright green thin-walled cells with hollow papillae, without propagula; Mexico, SW USA . . . . *Pseudocrossidium replicatum*
    3. Leaves relatively short, 0.7–1.2 mm, ovate to ovate-deltoid, apex broadly acute; ventral costal surface convex; guide cells 2–3; margins revolute 1 time, of undifferentiated cells, sometimes with rhizoidal and costal propagula; southern California, American NW, Arctic, and Greenland. . . . . *Pseudocrossidium obtusulum*

Pseudocrossidium revolutum is a European species with oblong-lanceolate to ligulate upper leaves, more strongly and more narrowly revolute margins extending nearly to the leaf base, margins as seen in section 1 1/2 times revolute with leaves strongly twisted and inrolled when dry. The leaf mucro is not stout and is shorter than in *P. obtusulum*, whose leaves are imbricated or only somewhat twisted when dry. The perichaetial leaves are strongly differentiated in *P. revolutum* and there is no record of propagula in this species, whereas the perichaetial leaves of the occasionally gemmiferous *P. obtusulum* are weakly differentiated or undifferentiated.

Pseudocrossidium obtusulum is rare in the Arctic (Zander in preparation) but distributed from Greenland, the Northwest Territories, and Alaska south to the Yukon, British Columbia, Oregon, and southern California just north of the Mexican border (map in Tan et al. 1981). In an extensive dry-steppe vegetational study by McIntosh (1986), the species was reported as locally common in the interior of British Columbia. The Montana station is an inland extension of its previously recorded range. McIntosh's description of the area as the Cordilleran steppe or shrub-steppe is extended eastward to southern Wyoming and Colorado, based on Daubenmire (1978). The area of the collections presently reported also represents the steppe conditions as characterized in McIntosh's south central British Columbia study. It is probably also controlled by the rain-shadow effect of the western mountains. No rhizoidal tubers as described and illustrated by Tan et al. (1981) were observed in the Montana collections.

As to *Pseudocrossidium obtusulum* belonging to floristic elements with distinctive distribution patterns, the reports of *P. revolutum* by McIntosh as a western North American–Eurasian species must be revised as *P. revolutum* has been excluded from the North American flora. That species would now be characterized as a Eurasian species. *Pseudocrossidium obtusulum* would then belong to McIntosh's western North American–western Eurasian element, since this species occurs from the Arctic to southern California and 2 stations in what one might expect to be temperate steppe conditions in central Germany and southern Sweden (Tan et al. 1981). Schofield (1980) discusses the disjunct flora of western North



Figs. 1–5. 1, *Pseudocrossidium hornschuchianum*; 2, *P. crinitum*; 3, *P. replicatum*; 4, *P. obtusulum*; 5, *P. revolutum* (from European material), showing the relative size of the perichaetial leaf to vegetative leaves. Scale bars: leaves, a = 0.5 mm; cross sections, b = 100 μm.

America and Europe, describing species that are widespread in America, such as *P. obtusulum* discussed here, but which are "restricted to few sites . . . throughout Europe." It is apparent that this species is an element of this disjunct distribution. "The absence of these and other species from most of Asia . . . strongly implies that these disjuncts have been isolated for many thousands of years, at least" (Schofield 1980).

The specimens were collected on very fine sandy loam composed of 53% sand, 40% silt, and 7% clay with a bulk density of 1.35 g/cm^3. Although volcanic ash deposits occur in the region nearby, that substrate was absent from the soil where specimens were collected. The site is in dryland sagebrush–bunchgrass habitat with precipitation varying from 8 to 20 inches/yr. Plants were growing on a vertical face just above the waterline of a large irrigation canal, and consequently the soil is continuously moist for nearly 5 months, from May to September, and extremely dry during the other 7 months. *Didymodon vinealis* (Brid.) Zand. var. *vinealis* was associated with the specimens.

Although *Pseudocrossidium obtusulum* has gemmae in North America, it fruits, and richly so, only in Greenland.

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STICK NESTS ON A BUILDING AND TRANSMISSION TOWERS USED FOR NESTING BY LARGE FALCONS IN UTAH

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ABSTRACT.—Large falcons (genus *Falco*) do not build their own nests and, in North America at least, usually nest on high cliffs. Occasionally they nest in abandoned stick nests built by another large bird on the cliff. In Asia and particularly South Africa, they sometimes nest in stick nests on electrical power transmission towers. This use of electric transmission towers was recently (1980) reported for the Prairie Falcon (*Falco mexicanus*) in North America but is unknown, except for 1 anecdotically documented use of an "electric-power pole" at the turn of century in California, for the Peregrine Falcon (*Falco peregrinus*) in North America. Here we report such nesting of the peregrine in North America and additional tower nestings for the Prairie Falcon.

Key words: electric transmission towers, Peregrine Falcon nesting, Prairie Falcon nesting, Falco peregrinus, Falco mexicanus.

Several species of raptors, primarily the buteos (*Buteo sp.*), ospreys (*Pandion*) and eagles (*Aquila*), and also the Common Raven (*Corvus corax*), use electric power transmission towers as nesting platforms and substrates (Steenhof et al. 1993, Blue 1996). Most of these species, however, build their own stick nests on towers. Frequency of use of towers varies from region to region and may, in part, have to do with learning within a local population that such structures are appropriate for nesting. Frequently, newly erected transmission lines cross regions where historically a species was absent as breeders, for there were no structures for nest sites, and thus use of such towers may then allow that species to move into an area locally and exploit a previously unused food source (White and Tanner-White 1988). Use of such situations thus confers a selective advantage to individual pairs. Although falcons do not build their own nests, they frequently use stick nests, generally on cliffs, that were abandoned by the original builders.

Nesting by large falcons in abandoned stick nests of other birds on electric power transmission structures is not uncommon in the eastern hemisphere. As an array of examples, stick nests on power transmission poles are used (rarely) by the Black Falcon (*Falco subniger*) in Australia (Marchant and Higgins 1993, del Hoyo et al. 1994), more frequently by the Saker Falcon (*Falco cherrug*) in Mongolia (Ellis et al. 1995) and the Ukraine (del Hoyo et al. 1994, S. Sorokin and V. Flint personal communications) and Laggar Falcon (*Falco jugger*) in India (Rishad Maoroji unpublished manuscript), and commonly by the Lanner Falcon (*Falco biarmicus*) in South Africa (Tarboton and Allan 1984). In the latter study, of 157 nesting Lanner Falcon pairs in the former Transvaal Province, 22.3% used stick nests on transmission towers and 1.3% used stick nests on buildings. In stark contrast, however, in North America the use of this combination of stick nest and transmission tower or building is very rare; in fact, there are no published reports, to our knowledge, of Peregrine Falcon (*Falco peregrinus*) using stick nests on transmission towers for nesting. There is, however, a record early in this century from California of a peregrine nest on a "platform on an electric-power pole," but it was not documented adequately enough in the literature to interpret what "platform" meant (R.M. Bond in letter to Hickey and Anderson 1969:18). The peregrine nest on Osprey (*Pandion haliaetus*) nests on 7-m-tall navigation guidance towers on Pacific coastal Baja California (J.B. Platt personal communication) "approximates" the hack tower discussed below. There are, however, at least 2 recently published records of the Prairie Falcon (*Falco mexicanus*) using transmission towers, 1 in New Mexico

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(Blue 1996) and 1 in Nevada (Roppe et al. 1989). In mid-latitude North America both species, particularly the peregrine, typically nest in inaccessible locations on cliff faces that are usually in excess of about 16 m (ca 50 ft). On a cosmopolitan basis, however, the peregrine shows considerable flexibility in the use of different nesting substrata, even nesting on the ground.

Throughout the early 1970s and early 1980s the Utah Division of Wildlife Resources (UDWR) erected several structures around the edge of the Great Salt Lake (GSL) from which to release (hack) Peregrine Falcons in a reestablishment program. These structures were about 7 m tall with a platform approximately 2 × 2 m in size on which a nesting box was placed. Young released from the towers were bred in captivity by The Peregrine Fund. They had black anodized U.S. Fish and Wildlife Service (USFWS) bands placed on the left leg (LL) and either plastic colored bands or colored aluminum bands with characters (letters and/or numbers) on the right leg (RL). Peregrines returned to the towers as adults and began breeding on them 4 yr after the initial releases. Young produced on the towers had a silver aluminum USFWS band placed on the RL and, in some cases (after 1990), a black anodized, coded band on the LL. There was no evidence, through at least 1994, that falcons from the towers (either initially released there or raised there as young) reoccupied nesting cliffs that were historically used on the nearby mountains, some of which are as close as 10 km. The peregrines, however, seemed to prefer, and perhaps even compete for, towers or other similar structures.

During the early 1980s the GSL underwent an unprecedented rise in water level from 4203′ ASL to a historical high of 4212′ ASL, which approximately doubled its surface area. Most towers and buildings otherwise around the lakeshore were surrounded by water and therefore secure from human intrusion.

BUILDING-NESTING PEREGRINE FALCONS

In 1988 Paul received reports of a pair of peregrines defending the vicinity of the historic Bear River Clubhouse (used by a duck hunting club). The clubhouse had been surrounded by a dike to protect it from waters of the GSL and was surrounded by a vast shallow lake for approximately 3 km to the nearest land. The house was the only structure left standing after several years of flooding and shear ice; thus, it and surrounding trees had become a veritable mecca for birds. Paul confirmed the reports on 4 April 1988. Permission was obtained to place a nesting box, about 2/3 the size of a hack box, on the roof of the 2-story clubhouse in hopes that the falcons would use it. On 14 April the pair was still in the area, but it could not be determined whether they were using the nest box. On 5 May the site was again visited, and the female peregrine flew from the southwest corner of the building and perched nearby, protesting loudly. It was at this time that band information was obtained for both birds (female: LL black anodized band, RL green band; male: RL dark band—indicating that both were raised at hack boxes and the female was from The Peregrine Fund). After the agitated falcons quieted down, the female disappeared on the west side of the building. There, 2 wings of the clubhouse come together to form a narrow passage. On investigation, the female flushed from a raven's nest built on top of an electrical circuitry box, about 2.5 m above ground and shaded by the eaves of the building at the end of the passage. The nest contained a clutch of 4 eggs. Three young (2 males, 1 female) were hatched and eventually fledged. One male and the female are known to have survived to dispersal. The other male disappeared somewhat earlier but is assumed also to have dispersed. All young were leg-banded prior to fledging. The nearest artificial nesting tower was some 32 km S at the Harold Crane Wildlife Management Area.

TRANSMISSION-TOWER–NESTING PEREGRINES

Another Peregrine Falcon nest was located on a 340-Kv electric power transmission tower immediately adjacent to the Farmington Bay Waterfowl Management Area (FBWMA) on the eastern shore of the GSL, Davis County. Falcons were initially observed by SDB and a group of 11 other biologists from the UDWR on 19 May 1994 when the male flew near the nest in which the female was incubating. This and all subsequent observations were made from the ground using binoculars and spotting scopes. The falcons were using a raven's nest built at the intersection of the main part of the tower and the middle cross section (useable photos are not available, but see figure in Roope et al. 1989 and Fig. 1 herein for approximate nest placement). We believe the ravens that built the nest may have been forced from it by the peregrines because a pair of ravens were attempting to build a nest on the next nearest transmission tower but were continually harassed by the peregrines. Since ravens typically have young nearly ready to fledge by mid-May, it is unlikely that the ravens would have newly moved into the area, especially to attempt building a nest so close to peregrines. Due to the location of the peregrine nest, the contents could not easily be seen except from an aircraft, so the initial number of eggs or young was unknown. A lone, large, downy nestling (ca 14 d old) was first observed in the nest on 26 June. The nest appeared to be very exposed most of the day to sun, wind, and rain. The female was seen frequently shading the nestling with her drooped wings during the hottest part of the day. In the absence of the female the nestling showed signs of heat stress. We last saw the young in the nest 26 July; it had fledged by 30 July. We judged it to be a female based on size.

Both adult birds had leg bands. The male had a black band (LL) and a red band (RL). The female had a black band (LL) and an aluminum band (RL). Based on the band configuration, the female was probably hatched at 1 of 7 nesting hack towers located around the GSL. The male may have been released by The Peregrine Fund as part of the reintroduction program. Several attempts to trap the adults to determine band numbers were unsuccessful because of the location of the tower relative to marshlands and appropriate locations to place a trap.

The nearest established nesting hack tower used by peregrines was at the Ambassador Gun Club about 11–12 km away. It was occupied by a pair of Barn Owls (*Tyto alba*) that same year (1994). As soon as the young owls were discovered, they were removed from the nesting box and placed in another nearby owl nest, but no peregrines attempted to nest in the box. We initially thought the pair of falcons using the stick nest on the power transmission tower was the same pair that had used the Ambassador hack tower in the past and had simply been prevented from nesting there by the presence of the early nesting Barn Owls. However, another pair of falcons was present in the Ambassador Club area and seen occasionally on the tower (R. Walters personal communications).

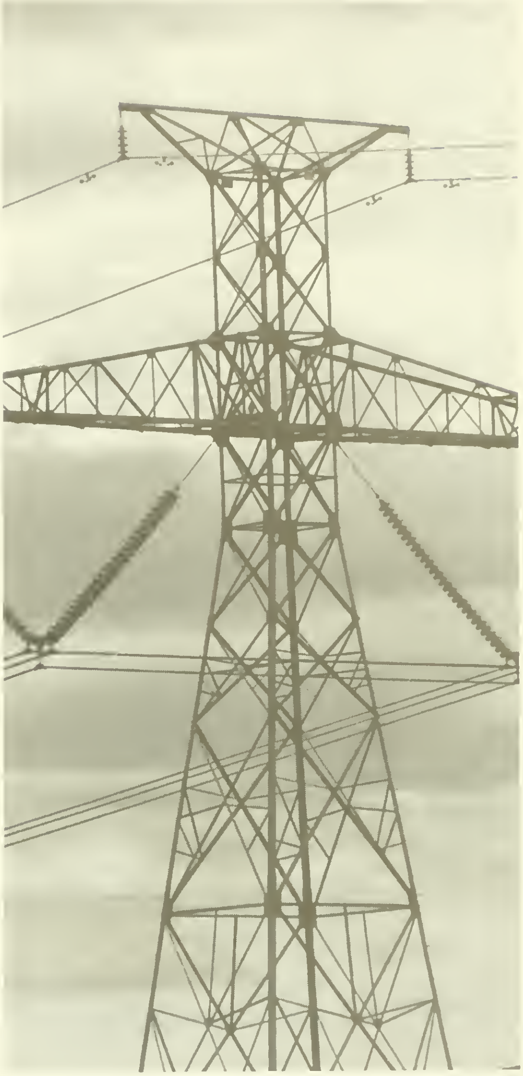

Fig. 1. Nest placement of the raven's nest used by the Prairie Falcon. Nest was in the center cross arm; the adult falcon can be seen standing on the edge of the nest. The placement is similar to that of the nests used by Peregrine Falcons near the GSL in 1994.

To encourage the pair to return to the same transmission tower area, we had hoped to place a nesting hack box on or near the same transmission tower, but were unsuccessful. The falcons were not observed trying to reoccupy the nest in 1995 even though a single female was there in early spring and a pair of ravens nested in the same nest in 1995.

In 1996 a pair of peregrines occupied the Ambassador Club nest hack tower and produced 3 young (males). The adult female was unbanded, and the male had no band on RL but we could not be certain about LL. During this same time Justin Dolling, superintendent of the FBWMA, found a pair of peregrines in May nesting in a raven's nest on the 1st horizontal bar of the 4th transmission tower about 0.8 km S of the FBWMA transmission tower used in 1994. Paul saw 2 young (ca 3 wk old) in the nest on 21 June, 2 were there on 7 July, and on 16 July the adults were seen with 1 female fledgling. The adult female had a black anodized aluminum band (LL) and a regular aluminum USFWS band (RL). The adult male was unbanded. The female could have been the same female that nested on the transmission tower in 1994 based on the band configuration. The males, however, were different birds because the 1994 male was banded.

In 1997 presumably the same pair (based on bands or lack of them) was back at the same transmission tower as in 1996; they occupied a different location on the tower, but it also was a raven's nest. The female was still incubating at the time this went to press.

TRANSMISSION-TOWER–NESTING PRAIRIE FALCONS

In mid-May 1994, Mark Allman, a falconer from Provo, and 2 colleagues found a pair of Prairie Falcons nesting in a raven's nest on a transmission tower on lines coming from the Intermountain Power Plant about 16 km NW of Delta, Millard County, Utah (Figs. 1, 2). The falcons defended the nest and tower. Allman was unable to return to the nest to determine its success. When we checked the area in September, we found a few molted Prairie Falcon feathers and some regurgitated pellets, like those cast from Prairie Falcons, below at least 1 other tower with raven nests farther west along the line, suggesting that perhaps a 2nd pair of falcons may also have used that stretch of transmission towers.

DISCUSSION

The use of stick nests on transmission towers by Peregrine Falcons represents a more significant behavioral shift for them than for Prairie Falcons that traditionally use deserted stick nests on cliffs. This behavior by peregrines is most likely a result of the use of hack towers in the reintroduction effort, the frequency and availability of raven's nests on power transmission towers, and the lack of "acceptable" cliff sites along the shores of the GSL; there are, however, abundant cliffs, some used historically by peregrines for nesting, 5–10 km E of GSL. Of interest is the fact that all but 1 of the Peregrine Falcons nesting on the transmission towers or buildings were from previous artificial nesting situations. The unbanded male at the transmission tower in 1996 and 1997 may have been produced from a normal cliff-nesting situation. If so, the fact that it would occupy a transmission tower and a raven's nest on the tower attests to the species' ecological amplitude in

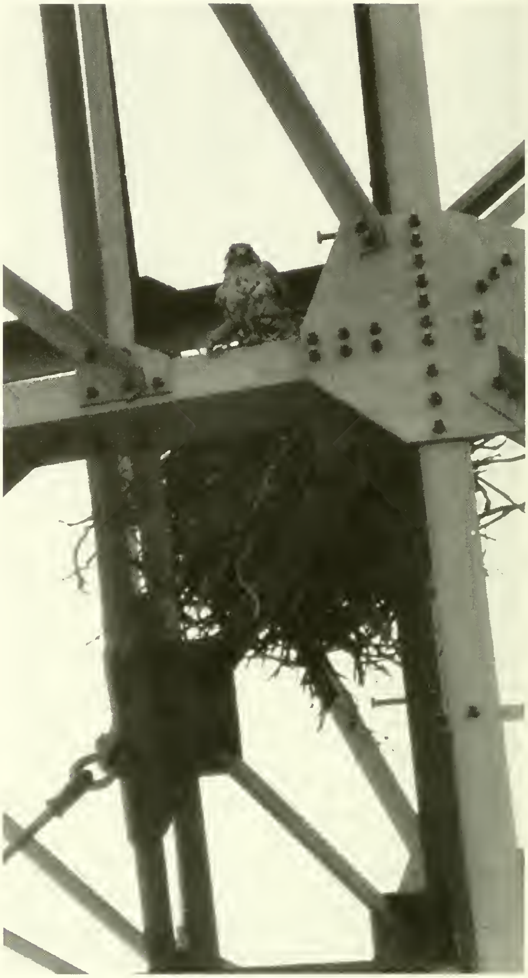

Fig. 2. View of the Prairie Falcon on the nest edge.

nesting. Alternatively, that male may simply have been raised at a hack tower that contained a stick at some more distant unknown release location outside of Utah where the young had not been banded.

Addendum: Peregrines were recently reported using similar pylon situations in Holland (1993) and Germany (1995) *in* Newsletter 23/24, 1996, World Working Group of Birds of Prey and Owls, B-U Meyburg, editor, Berlin, Germany.

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EFFECTS OF MYOFIBROGRANULOMA ON SERUM CALCIUM LEVELS IN WALLEYE (*STIZOSTEDION VITREUM*)

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ABSTRACT.—The effect of myofibrogranuloma (skeletal muscle degeneration) on serum calcium levels in spawning walleye (*Stizostedion vitreum*) was examined. Mean serum calcium levels for healthy male walleye (11.7 ± 1.5 mg/100 ml serum) was significantly lower ($P < 0.05$) than calcium levels for healthy female walleye (15.4 ± 1.8 mg/100 ml serum). Significant increases ($P < 0.1$) in serum calcium were seen between healthy male and myofibrogranuloma-diseased male walleye (13.6 ± 2.1 mg/100 ml serum) and between healthy and myofibrogranuloma-diseased female walleye (20.2 ± 3.7 mg/100 ml serum). Elevations seen in mean serum calcium levels suggest the muscle degeneration and subsequent granuloma formation in later stages of myofibrogranuloma have a significant effect on serum calcium.

Key words: calcium, walleye, myofibrogranuloma, colorimetric determination, Stizostedion vitreum.

Calcium (Ca) levels of osteichthyan extracellular fluids are regulated to a finer degree than those of more primitive fishes (Dacke 1979). Hormones from the pituitary, ultimobranchials, stannius corpuscles, and gonads affect osteichthyan Ca metabolism (Dacke 1979). Since Ca concentration is essential for cell membrane permeability to water, neuromuscular irritability and blood clotting, growth and enzyme reactions, it is less variable than other ions in serum (Urist and Van de Putte 1967).

Myofibrogranuloma (MFG) is a unique form of skeletal muscle degeneration recognized only in adult walleye (*Stizostedion vitreum;* Mayes 1976, Economon 1978, Holloway and Smith 1982). This myopathy is characterized by profound alterations of the trunk musculature produced by extensive hypertrophy of the muscle fibers (Economon 1978). Holloway and Smith (1982) noted 2 degenerative processes. The 1st and most pronounced lesion consisted of coagulation necrosis of muscle fibers accompanied by an inflammatory response and the formation of granulomas (muscle tumors). The 2nd was noninflammatory and characterized by focal areas of acute myolysis. Mineralization or calcification was evident in the central portion of some fibers in the more granular stage of degeneration (Economon 1978). Kelly et al. (1987) showed an increase in muscle Ca associated with myofibrogranuloma (55 times normal muscle fibers). Histochemical staining indicated relatively more Ca-positive fibers in normal muscle of MFG-positive fish and MFG-positive tissue than in muscle from healthy walleye (Kelly et al. 1987). Holloway and Shoemaker (1993) used X-ray technology to demonstrate increased opacity, presumably due to concentrated Ca in MFG-diseased tissue. The cause of MFG is unknown. Fisheries managers and anglers are concerned about the disease because the involved muscle has a yellow color with sandy texture. Anglers discard these fish.

Adult osteichthyans (bony fishes) exhibit seasonal variations in plasma Ca levels associated with breeding cycles (Dacke 1979). Sex differences in plasma Ca levels of fish were first reported by Hess et al. (1928). Booke (1964) found differences in the Ca levels of spawning male and female brook trout (*Salvelinus fontinalis*). Hunn (1972) presented values of various fishes, including spawning male walleye, from the upper Mississippi River. Our objective was to establish Ca values for spawning male, female, and MFG-diseased walleye using a simple colorimetric procedure.

MATERIALS AND METHODS

Spawning walleye were collected by gill and frame net from Merrit Reservoir, Nebraska (1991 and 1992), and Lake Sakakawea, North Dakota (1991). Only walleye greater than 500 mm total length were sampled to eliminate killing smaller fish that would not show macroscopic signs of disease. Blood was sampled via cardiac puncture with heparinized 10-ml syringe and 21-gauge needle. Centrifugation was carried out within 24 h to minimize sample hemolysis. Serum was placed in dry ice for transport and stored at −80°C until analyzed. Heavily hemolyzed samples were discarded. Walleye were filleted and examined with unaided eye for MFG. MFG-diseased fish were determined by observing yellow-colored, sandy-textured muscle.

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The procedure for measuring serum Ca concentration was modified from Fales (1953) by Oser (1965). We used the latter protocol, but serum and reagent volumes were halved due to small sample volume. A 1% stock Ca standard solution was prepared by dissolving 2.497 g calcium carbonate in 6 N hydrochloric acid and evaporating on a steam bath to dryness. The residue ($CaCl_2$) was then dissolved in distilled water to make 100 ml. A Ca standard (0.1 mg/ml) was prepared by diluting 1 ml of the stock Ca to 100 ml with 1.4 N sodium chloride. A light-sensitive stock solution of murexide was prepared by dissolving 0.25 g ammonium purpurate in 5 ml distilled water and 25 ml 95% ethanol. The working murexide solution was prepared by adding stock murexide solution to 100 ml 0.05 N sodium chloride until an OD of 0.39–0.48 was reached at 620 nm. The titrant was prepared by mixing 18 volumes of the working murexide solution, 1 volume of 0.14 N sodium chloride, and 1 volume of stock disodium dihydrogen ethylene-diaminetetraacetic acid (EDTA) solution (0.005 M EDTA). Titrant was mixed prior to each set of determinations, kept in brown bottles, and used within 1.5 h.

The principle of the procedure as described by Oser (1965) is that the Ca in serum mixed with murexide forms a red-colored complex in equilibrium with free Ca ions. Titration of the Ca-murexide complex with EDTA chelates frees Ca ions, causing the release of Ca ions from the complex. As the murexide ion : calcium murexide ratio increases, there is a shift in color from red to purple (endpoint). The procedure followed is described briefly: 0.25 ml of 0.14 N sodium chloride was placed in a blank cuvette, and equal amounts (0.25 ml) of serum and working Ca standard were placed in test and standard cuvettes, respectively. Then, 2.25 ml of working murexide and 0.5 ml of titrant were added to each cuvette and mixed. The spectrophotometer (Bausch and Lomb Spectronic 20) was set at 50% transmittance at 620 nm with the blank, and the test and standard cuvettes were then read. After this, 0.25 ml of titrant was added to each cuvette and the spectrophotometer reset at 50% transmittance with the blank, before reading the test and standard. This step (titration) was repeated and followed colorimetrically until the endpoint was reached (all serum Ca bound to EDTA). Calculations were then carried out using the following formula as described by Oser (1965) to determine serum Ca level:

$$\frac{\text{Volume of titrant for serum}}{\text{Volume of titrant for standard}} \times 10 = \text{mg Ca/100 ml serum}$$

A Student's *t* test compared mean serum Ca levels of healthy male and female walleye. Significance was determined at $P < 0.05$. Due to small sample size and differences between variances, healthy male walleye and MFG-positive male walleye as well as healthy female walleye and MFG-positive female walleye were compared by unequal variance *t* test (Sokal and Rohlf 1981). The critical significance level was $P < 0.10$ for tests between MFG-positive and healthy male and female walleye because of the low numbers of MFG-positive fish (6 males and 4 females).

RESULTS AND DISCUSSION

Selected serum Ca titration curves (standard, spawning female [NB201], spawning male [0066], MFG-positive spawning female [0043], and MFG-positive spawning male [0252]) are shown in Figure 1, and serum Ca concentrations are described in Table 1 for healthy and MFG-positive walleye. A significant difference was found between serum Ca levels of male and female walleye ($P < 0.05$). Serum Ca levels of male walleye differed significantly from mean serum Ca levels of MFG-positive male walleye ($P < 0.10$). A significant difference was found between serum Ca levels of healthy female walleye and MFG-positive female walleye ($P < 0.10$).

Serum Ca values were higher in this study than in others (Table 2). One explanation may be species differences. Hunn (1972) examined spawning male walleye from the upper Mississippi River and found serum Ca lower (9.52

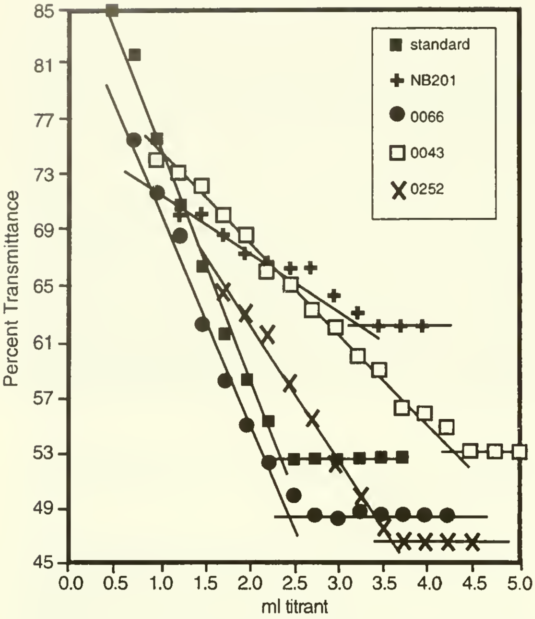

Fig. 1. Selected Ca titration curves of serum collected from spawning walleye (*Stizostedion vitreum*) using a colorimetric assay (standard = 0.1 mg Ca/ml, NB201 = healthy female, 0066 = healthy male, 0043 = MFG-positive female, 0252 = MFG-positive male).

mg/100 ml) than our mean value (11.68 mg/100 ml) for spawning male walleye. This may be a result of the blood-sampling procedure (caudal peduncle puncture vs. cardiac puncture), which is known to influence other blood parameters (e.g., serum enzyme levels; Hille 1982), or simply differences between river and reservoir fish. Low serum Ca levels in paddlefish (*Polyodon spathula*) suggest physiological hypocalcemia, and in this respect paddlefish show phylogenetic affinity to sturgeons (Grant et al. 1970). The low levels seem to support Urist and Van de Putte's (1967) suggestion that hypocalcemia is related to the absence of a bony skeleton; however, gravid female white sturgeon (*Acipenser transmontanus*) exhibit increased serum Ca. Low serum Ca determined for channel catfish (*Ictalurus punctatus;* 9.2 mg/100 ml) may be a result of obtaining fish from culture ponds rather than from natural waters (Warner and Williams 1977).

Various techniques were used to determine serum Ca levels, which may have resulted in differences noted. Methods of Ca determination include automated methods (Warner and Williams 1977), colorimetric methods (Field et al. 1943, Shell 1961, Booke 1964), and atomic absorption spectrophotometry (Grant et al. 1970, Hunn 1972). The colorimetric method described by Fales (1953) determined total serum Ca (ionic plus protein-bound), and he found excellent agreement with the method of Clark and Collip (1925), which also measured total Ca. In addition, the method is inexpensive (low cost of equipment [Spectronic 20] and reagents).

The difference between serum Ca levels of healthy male and female walleye was due to egg production. Sex differences in Ca levels in osteichthyan fish were first reported by Hess et al. (1928), who found a range of 9–12.5 mg/100 ml serum in male cod (*Gadus morhua*), while mature females had a range of 12.7–29 mg/100 ml serum. Dacke (1979) suggested that hypercalcemia is related to the influence of estrogen and ovarian follicle maturation, which stimulate synthesis of yolk protein and hence an increase in protein-bound plasma Ca. Urist and Van de Putte (1967) found similar results for spawning sturgeon. Spawning brook trout females also exhibited increased levels of Ca (Booke 1964). Hunn et al. (1992) found Ca levels were significantly higher in gravid female than in male golden trout (*Oncorhynchus aguabonita*).

Dacke (1979) stated that Ca levels throughout the osteichthyan subphylum are regulated within narrow limits. This is accomplished, in part, by exchange with Ca in the aquatic environment and by exchange with bone Ca. Oser (1965) stated slight variations in normal levels of serum Ca are indicative of pathology such as bone abnormalities and muscle tumors. Even though our sample sizes of MFG-positive fish were small, elevations were seen in Ca levels of MFG-positive male and female walleye. These elevations suggest Ca is highly regulated in walleye and that MFG has a significant effect on serum Ca levels, probably resulting from acute myolysis (Holloway and Smith 1982) leading to increased extracellular Ca.

ACKNOWLEDGMENTS

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TABLE 1. Serum Ca (mg/100 ml serum) of healthy and MFG-positive spawning male and female walleye (*Stizostedion vitreum*) from Merrit Reservoir, NE, and Lake Sakakawea, ND.

Fish	Sample size	Mean ± *s*[1]	Range
Healthy female	20	$15.4 \pm 1.8^{a,\dagger}$	11.9–19.5
Healthy male	18	$11.7 \pm 1.5^{b,\dagger}$	9.1–14.6
MFG-positive female	4	$20.2 \pm 3.7^{\ddagger}$	17.1–25.4
MFG-positive male	6	$13.6 \pm 2.1^{\ddagger}$	11.5–16.8

[1] Means with different alphabetical letter superscripts were significantly different between sexes at $P < 0.05$. The means marked with different symbols were significantly different within the same sex (i.e., healthy female compared to MFG-positive female and healthy male compared to MFG-positive male) at $P < 0.10$.

TABLE 2. Published serum Ca values (mg/100 ml serum) for freshwater fishes.

Author(s)	Sample size Species	Mean ± *s*	Range
Warner and Williams (1977)	107	9.2 ± 2.65	3.9–4.5
	Ictalurus punctatus		
Field et al. (1943)	5–10	11.5	9.45–14.77
	Cyprinus carpio		
Shell (1961)	30 (pooled sample)	—	10.2–19.5
	Micropterus dolomieui		
Grant et al. (1970)	3 female	7.46	—
	8 male	7.72	—
	Polyodon spathula		
Grant et al. (1969)	14 males	12.6	
	Carassius auratus		
Urist and Van de Putte (1967)	6 gravid females	18.4	—
	4 male/nongravid female	7.2	—
	Acipenser transmontanus		
Hunn (1972)	9 male	9.52 ± 0.3	—
	Stizostedion vitreum		
Booke (1964)	females	—	5.54–27.79
	males	—	6.34–10.65
	Salvelinus fontinalis		

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HELMINTHS FROM THE SONORAN SPOTTED WHIPTAIL, *CNEMIDOPHORUS SONORAE*, AND THE WESTERN WHIPTAIL, *CNEMIDOPHORUS TIGRIS* (SAURIA: TEIIDAE), FROM SOUTHERN ARIZONA WITH COMMENTS ON *ABBREVIATA TERRAPENIS* (NEMATODA: PHYSALOPTERIDAE)

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Key words: Cnemidophorus sonorae, Cnemidophorus tigris, *Teiidae, helminths, Nematoda, Cestoda, Acanthocephala, Arizona.*

Cnemidophorus sonorae Lowe and Wright, 1964, the Sonoran spotted whiptail, occurs from southeastern Arizona to northeastern Sonora and east to western New Mexico; *Cnemidophorus tigris* Baird and Girard, 1852, the western whiptail, ranges from Oregon and Idaho south through California to Baja California and Coahuila, México, and eastward to western Colorado, New Mexico, and Texas (Stebbins 1985). Helminths have been previously reported from *Cnemidophorus sonorae* by McAllister (1992) and *Cnemidophorus tigris* by Grundmann (1959), Babero and Matthias (1967), Telford (1970), Specian and Ubelaker (1974a, 1974b), Benes (1985), and Lyon (1986).

Abbreviata terrapenis (Hill 1945) Morgan, 1945 was originally described from specimens taken from 7 ornate box turtles (*Terrapene ornata*) collected from widely separated points in Oklahoma (Hill 1945). The 1st lizard host to be reported for this helminth was *Sceloporus jarrovii*, also collected from widely separated points in Arizona, New Mexico, and México (Goldberg et al. 1995, 1996). The purpose of this paper is to report on a helminthological examination of *Cnemidophorus sonorae* and *Cnemidophorus tigris* from southern Arizona and the presence of *A. terrapenis* in these 2 additional lizard hosts.

Twenty-one female *Cnemidophorus sonorae* (mean snout-vent length [SVL] = 73.2 mm ± 5.6 *s*, range 60–80) and 82 *Cnemidophorus tigris* (28 females, 54 males; mean SVL = 65.6 mm ± 10.1 *s*, range 34–82 mm) were borrowed from the herpetology collections of the Natural History Museum of Los Angeles County (LACM) and the University of Arizona (UAZ) and examined; collection data are given in the Appendix. The lizards were originally preserved in 10% formalin or Bouin's fixative and stored in 70% ethanol. The body cavity was opened and the gastrointestinal tract was excised by cutting across the esophagus and rectum. The esophagus, stomach, small intestines, and large intestines were slit longitudinally and examined separately under a dissecting microscope. The body cavity and liver were also examined. Each helminth was removed and initially placed in a drop of glycerol on a glass slide. Nematodes were identified from these temporary mounts. Cestodes were stained with hematoxylin, mounted in balsam, and identified. Acanthocephalans were cleared in xylene, mounted in balsam, and assigned to genus. Terminology usage is in accordance with Margolis et al. (1982).

Cnemidophorus sonorae was found to harbor 2 species of cestodes, *Oochoristica bivitellobata* Loewen, 1940 and *O. macallisteri* Bursey and Goldberg, 1996; and 3 species of nematodes, *Abbreviata terrapenis, Pharyngodon warneri* Harwood, 1932, and *Thubunaea cnemidophorus* Babero and Matthias, 1967. *Cnemidophorus tigris* was found to harbor 1 species of cestode, *O. bivitellobata*; 2 species of nematodes, *A. terrapenis* and *P. warneri;* and cystacanths of a species of Acanthocephala, *Centrorhynchus* sp. Prevalences and mean intensities for these helminths are given in Table 1. The infection prevalence between males and females of *C. tigris* was not significantly different (for *A. terrapenis*, $\chi^2 = 0.17$, 1 df, $P > 0.05$; for *P.*

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TABLE 1. Gastrointestinal helminths of 21 *Cnemidophorus sonorae* and 82 *C. tigris* from Pima County, AZ.

Helminth	*Cnemidophorus sonorae* Prevalence (%)	Mean intensity (range)	Site[1]	*Cnemidophorus tigris* Prevalence (%)	Mean intensity (range)	Site[1]
Oochoristica bivitellobata	5	6.0	c	1	3.0	c
Oochoristica macallisteri	5[2]	2.0	c	—	—	—
Abbreviata terrapenis	76[2]	8.0 (1–24)	a,b	86[2]	14.3 (1–61)	a,b,c,d
Pharyngodon warneri	14[2]	22.7 (4–55)	c,d	42	50.3 (1–220)	d
Thubunaea cnemidophorus	5[2]	2.0	b	—	—	—
Centrorhynchus sp.	—	—	—	4	1.0	b

[1] a = esophagus, b = stomach, c = small intestine, d = large intestine
[2] new host record

warneri, $\chi^2 = 0.21$, 1 df, $P > 0.05$). *Cnemidophorus sonorae* is a new host record for *O. macallisteri*, *A. terrapenis*, *P. warneri*, and *T. cnemidophorus*; *C. tigris* is a new host record for *A. terrapenis*. Helminths were placed in vials of alcohol and deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland (accession numbers in Appendix).

Oochoristica bivitellobata, *Pharyngodon warneri*, and *Thubunaea cnemidophorus* have been previously reported in North American lizards (Table 2) and may be limited to teiid lizards. The occurrence of *T. cnemidophorus* in the crotalid snakes *Crotalus cerastes*, *C. mitchelli*, and *C. scutulatus* by Babero and Emmerson (1974) needs further study to determine if the snakes are indeed hosts, or if the parasites were present in lizards that the snakes had ingested. McAllister (1992) questioned the determination of *O. bivitellobata* in *Sceloporus undulatus* and suggested that it probably is *Oochoristica scelopori*; thus, *S. undulatus* is not included in Table 2. Species of *Centrorhynchus* typically use arthropods (probably insects) as intermediate hosts and primarily birds of prey as definitive hosts (Petrochenko 1958). The occasional presence of a cystacanth in the stomach of an insectivore could be expected. One nematode not found in these lizards, but frequently associated with teiid lizards, is *Parathelandros texanus* Specian and Ubelaker, 1974. This helminth may be limited to west Texas (see Baker 1987).

This is the first report of adult *Abbreviata terrapenis* from teiid lizards, although larvae of *Abbreviata* sp. have been reported from *C. sexlineatus* by McAllister, Trauth, and Conn (1991). Larvae of *Abbreviata* sp. have also been reported from the crotaphytid lizard *Crotaphytus collaris* and the phrynosomatid lizard *Sceloporus undulatus* (Morgan 1941, McAllister and Trauth 1985). Adults of *Abbreviata terrapenis* have previously been reported from *Sceloporus jarrovii* in Arizona, New Mexico, and México (Goldberg et al. 1995, 1996). This is also the 1st report of *O. macallisteri* from a teiid lizard, although unidentified species of *Oochoristica* have been reported from *Cnemidophorus dixoni*, *C. gularis*, and *C. tesselatus* (McAllister 1990a, 1990d, McAllister, Cordes, and Walker 1991). In Arizona, Benes (1985) reported *Oochoristica* from *Cnemidophorus tigris*, *Coleonyx variegatus*, *Phrynosoma solare*, *Sceloporus magister*, and *Uta stansburiana*, but did not identify the species.

Abbreviata terrapenis is a heteroxenous physalopterid helminth with an indirect life cycle involving an insect intermediate host (Anderson 1992). Echternacht (1967) reported that termites are the major dietary component for *C. sonorae* and *C. tigris* from the Santa Rita Mountains, Pima County, Arizona, representing over 90% of all prey organisms consumed. Mitchell (1979) reported a predominance of termites in the diets of *C. sonorae* and *C. tigris* in Cochise County, southeastern Arizona. Vitt and Ohmart (1977) similarly found that termites compose 76% of the diet of *C. tigris* living along the Colorado River in western Arizona. Pianka (1970) reported that, while southern *C. tigris* populations eat large quantities of termites, northern populations (Idaho, Nevada, Utah) utilize other food types and consume few termites. If termites serve as intermediate hosts for *Abbreviata terrapenis*, low frequencies of these insects in the diets of *C. tigris* from northern populations might account for the absence of *A. terrapenis* in the studies of these populations by Grundmann (1959), Babero and Matthias (1967), and Lyon (1986).

TABLE 2. Reports of *Oochoristica bivitellobata*, *Pharyngodon warneri*, and *Thubunaea cnemidophorus* from teiid lizards.

Helminth	Host	Locality	Prevalence	Reference
Oochoristica bivitellobata	*Cnemidophorus burti*	Arizona	1/57 (2%)	Goldberg and Bursey 1989
	C. dixoni	Texas	9/58 (16%)	McAllister, Cordes, and Walker 1991
	C. exsanguis	New Mexico, Texas	7/87 (8%)	McAllister 1990c
	C. flagellicaudus	New Mexico	5/23 (22%)	McAllister 1992
	C. gularis	New Mexico, Texas	3/289 (1%)	McAllister 1990d
		Texas	1/83 (1%)	McAllister et al. 1995
	C. hyperythrus	California	5/104 (5%)	Bostic 1965
	C. inornatus	Arizona	10/78 (13%)	Goldberg and Bursey 1990
	C. neomexicanus	New Mexico, Texas	7/61 (11%)	McAllister 1990b
	C. sexlineatus	Kansas	91/144 (63%)	Loewen 1940
		Nebraska	3/3 (100%)	Brooks and Mayes 1976
			2/64 (3%)	Shoop and Janovy 1978
		South Dakota	13/23 (57%)	Dyer 1971
	C. sonorae	Arizona	1/16 (6%)	McAllister 1992
	C. tesselatus	Texas	3/27 (11%)	McAllister 1990a
	C. tigris	California	13/49 (27%)	Telford 1970
		Idaho	13/32 (41%)	Lyon 1986
		Nevada	5/97 (5%)	Babero and Matthias 1967
		Utah	5/7 (71%)	Grundmann 1959
	C. uniparens	Arizona	8/31 (26%)	Goldberg and Bursey 1990
	C. velox	Colorado	not stated	Douglas 1966
		New Mexico	2/37 (5%)	McAllister 1992
Pharyngodon warneri	*C. exsanguis*	New Mexico, Texas	10/87 (11%)	McAllister 1990c
	C. gularis	Oklahoma, Texas, Mexico	69/289 (24%)	McAllister 1990d
		Texas	2/83 (2%)	McAllister et al. 1995
	C. inornatus	Arizona	18/78 (23%)	Goldberg and Bursey 1990
		Texas	not stated	Specian and Ubelaker 1974a
	C. laredoensis	Texas	5/22 (23%)	McAllister et al. 1986
	C. neomexicanus	New Mexico, Texas	2/61 (3%)	McAllister 1990b
	C. sexlineatus	Texas	2/4 (50%)	Harwood 1932
		South Dakota	19/23 (83%)	Dyer 1971
		Arkansas	15/51 (29%)	McAllister, Trauth, and Conn 1991
	C. tesselatus	Texas	4/27 (15%)	McAllister 1990a
	C. tigris	Utah	5/7 (71%)	Grundmann 1959
		Arizona, Nevada	63/100 (63%)	Babero and Matthias 1967
Thubunaea cnemidophorus	*C. tigris*	Nevada	9/87 (10%)	Babero and Matthias 1967
	C. burti	Arizona	2/57 (4%)	Goldberg and Bursey 1989
	C. sexlineatus	Arkansas	3/51 (6%)	McAllister, Trauth, and Conn 1991

It has been shown that *Skrjabinoptera phrynosoma*, also a member of the Physalopteridae and a common parasite of *Phrynosoma* spp., is dependent upon ants (*Pogonomyrmex* sp.) as intermediate hosts (Lee 1957). The possibility that termites may serve as intermediate hosts of *A. terrapenis* needs to be investigated. Such information would be helpful in determining distribution patterns of *A. terrapenis*.

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APPENDIX
MUSEUM ACCESSION NUMBERS

University of Arizona

Cnemidophorus sonorae (N = 21 [all females]) Sabino Canyon (883 m elevation, 32°20′N, 110°49′W), Santa Catalina Mountains, Pima County, Arizona, collected 1953 (UAZ 4810–12, 4861), 1960 (10903, 10971), 1961 (11034), 1964 (15252, 15258, 15471, 15541, 15708), 1967–1969 (20666–67, 20677, 20681, 20687, 29637, 30087, 30090, 30682).

Natural History Museum of Los Angeles County

Cnemidophorus tigris (N = 77 [27 females, 50 males]) foothills Santa Catalina Mountains (822 m elevation, 32°20′N, 110°07′W), Pima County, Arizona, collected 1962 (LACM 143588), 1963 (LACM 143587, 143589), 1964 (LACM 143590–93), 1966 (LACM 143586, 143594–634), 1969 (LACM 143558–85); (N = 5 [1 female, 4 males]) Avra Valley (457 m elevation, 32°20′N, 111°20′W), Pima County, collected 1964 (LACM 14365–69).

U.S. National Parasite Collection

Cnemidophorus sonorae: *Oochoristica bivitellobata*, 86861; *Oochoristica macallisteri*, 86862; *Abbreviata terrapenis*, 86863; *Pharyngodon warneri*, 86864; *Thubunaea cnemidophorus*, 86865.

Cnemidophorus tigris: *Oochoristica bivitellobata*, 86866; *Abbreviata terrapenis*, 86867; *Pharyngodon warneri*, 86868; *Centrorhynchus* sp. (cystacanth), 86869.

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RANGE EXPANSION OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) INTO URBAN AND AGRICULTURAL AREAS OF UTAH

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Key words: range expansion, urban areas, Utah, white-tailed deer.

Numbers of white-tailed deer (*Odocoileus virginianus*) in the United States have increased to an unprecedented level over the past 50–60 yr (McCabe and McCabe 1984, Curtis and Richmond 1992, Harlow and Guynn 1994). During this time range expansion by white-tailed deer has occurred in portions of the western United States, regions dominated historically by mule deer (*O. hemionus;* Martinka 1968, Baker 1984, Wiggers and Beasom 1986, Mackie 1995). Because white-tailed deer adapt readily to man-altered environments, range expansion has been linked with land-use changes brought about by humans (Baker 1984, Dusek et al. 1989, Wood et al. 1994). Accordingly, range expansion into the West by white-tailed deer has been most conspicuous in agricultural (Kufeld and Bowden 1995) and urban (Vogel 1989) environments, where white-tailed deer may now outnumber mule deer.

White-tailed deer currently occupy the largest geographic range of any native terrestrial mammal in North America (Pagel et al. 1991). Their present distribution in the United States includes every contiguous state (Halls 1978, Hall 1981, Baker 1984, Smith and Rhodes 1994), although Halls (1978:43) and Hesselton and Hesselton (1982:878) question whether their distribution into Utah is verifiable. Undocumented sightings of white-tailed deer have been reported in northern Utah in the last 50–60 yr. However, we have been unable to find substantial evidence (e.g., harvest records, photographs) that confirmed their existence. Durrant (1952:456) did not list white-tailed deer as a species occurring in Utah but did suggest that their presence has been reported in the literature and that "some persons think they occasionally see them." Durrant, however, did not provide any references. Hall and Kelson (1959:1011) list an account of white-tailed deer north of Ogden, Utah. They reference Miller and Kellogg (1955:802), who in turn reference Bailey (1932). Bailey, however, does not mention Utah in his account. Consequently, confirming the existence of white-tailed deer in Utah has been problematic and, until now, appears not to have been documented definitively.

This note documents our observations of 2 white-tailed deer in Cache Valley of northern Utah. On 8 February 1996 we sighted and photographed a male white-tailed deer in an urban environment near Logan (UTM 4623500N 433100E). This deer accompanied a radio-collared doe mule deer, and we were therefore able to relocate him until 10 April, at which time he was killed by an automobile. During those 2 mon, this deer confined his activities to a 1-km^2 area, and we frequently observed him from ≤ 20 m away. We identified him as a white-tailed deer based on his white underparts (tail, chin, and neck), the distinctive white band around his muzzle, the white rings around his eyes, the white fringe around his large tail, as well as his tail-flagging behavior when startled or in flight. When in flight, this deer galloped, a gait that differs from the stot of a mule deer and the bound of a whitetail–mule deer hybrid (Lingle 1993). His antlers (3 pt × 2 pt), also characteristic of white-tailed deer, were formed from 1 main beam curving outward and forward; the unbranched tines extended from this main beam. After he died we estimated his age to be 1.5–2 yr, based on tooth eruption and wear.

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On 2 March 1996 we sighted a 2nd white-tailed deer in an agricultural environment near Smithfield (UTM 4635200N 431100E), 11.9 km from the 1st deer. Using binoculars from an elevated position, we observed this deer for 2 h at a distance of 50–200 m. Because this deer did not have antlers, nor was there any indication of antler loss, we concluded it was a female. We did not observe this deer urinate, which would have provided further evidence of sex. We identified her as a white-tailed deer based on the same defining characteristics listed above, except antler shape. Throughout the observation period this deer associated with a group of 16 mule deer, an occurrence that accentuated her defining behavioral and morphological characteristics. Based on her relatively large size and coloration pattern, we believe she was an adult (≥ 2.5 yr).

Although both deer appeared to be purebreds based on their behavioral and morphological characteristics, it is possible that they could have been whitetail–mule deer hybrids. Hybrids will frequently exhibit intermediate morphological and behavioral traits, but these traits are not always obvious, and accurate identification may be difficult in the field (Day 1980). Genetic studies (e.g., protein electrophoresis or mitochondrial DNA analysis) provide more definitive evidence of hybridization (Cronin et al. 1988), but we did not perform these studies. Consequently, our conclusion that these 2 deer were purebred should be viewed with caution.

If the unconfirmed sightings of white-tailed deer within the past 60 yr were accurate, the animals we observed would not represent the 1st record of this species to exist in the state. To our knowledge, however, these are the first 2 documented accounts of white-tailed deer in Utah. Although we cannot ascertain how these 2 deer arrived in Cache Valley, it is possible that they, or their progenitors, emigrated from either Wyoming or Idaho. White-tailed deer in Wyoming appear to be increasing and expanding their ranges westward through agricultural and riparian areas (Pauley and Lindzey 1993). Within the past 10 yr, sightings of white-tailed deer and hybrids have occurred in the southwest corner of Wyoming near Green River and Kemmerer (T. Christiansen personal communication). In Idaho, numbers of white-tailed deer have increased around Idaho Falls within the past 6 yr (R. Smith personal communication), and they are known to exist as far south as American Falls (C. Anderson personal communication).

White-tailed deer may be better adapted than mule deer to survive in intensively cultivated agricultural and urban areas (Vogel 1989). We therefore speculate that changes in land-use practices related to agriculture and urbanization brought about by man during the last century have created patches of habitat in Utah that appear to be suitable for white-tailed deer. The environments in which we observed these 2 white-tailed deer provide preliminary support for this speculation. As the connectivity of urban and agricultural developments increases and the open landscape of the West is fragmented, continued expansion by white-tailed deer into formerly unoccupied regions is conceivable.

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ESTABLISHMENT OF THE TUNGID FLEA, *TUNGA MONOSITUS* (SIPHONAPTERA: PULICIDAE), IN THE UNITED STATES

Michael W. Hastriter[1]

Key words: Tunga monositus, *Siphonaptera, distribution.*

The flea genus *Tunga*, containing 9 species, has a Neotropical origin occurring on Edentates (*T. bondari* Wagner, *T. penetrans* Linnaeus, *T. terasma* Jordan, *T. travassosi* Pinto & Dreyfus) and rodents of the families Muridae [*T. caecata* (Enderlein), *T. callida* Li & Chin, *T. caecigena* Jordan & Rothschild] and Cricetidae (*T. libis* Smit, *T. monositus* Barnes & Radovsky, 1969). Introduced specimens of *T. penetrans* have been reported several times in the United States, but established populations have not been documented. Of particular interest, eggs and adults of *T. penetrans* were reportedly taken from the remains of a dog removed from the cists of Basket-Maker Indian excavations in northeastern Arizona (Wilson, 1933), but Smit (1960) examined 4 of Wilson's slide preparations and was unable to verify such findings.

During a recent collection trip to southwestern Utah (11–13 January 1997), I collected 7 specimens of *T. monositus* adjacent to the southwest boundary of Zion National Park, Washington County, Utah (elevation 1275 m). Previously this species had been reported only at the type locality of Cape of San Quintin (30°27′N, 116°12′W), Baja California, Mexico, by Barnes and Radovsky (1969) and on San Martin Island (elevation sea level–200 m). Specimens on San Martin Island originally reported as *T. caecata* by Banks (1964) later proved to be *T. monositus* according to Barnes and Radovsky (1969).

This paper presents the 1st record of *Tunga* (*T. monositus*) established in the continental United States. Twenty-one rodents were examined and 6 (29%) harbored this flea. Positive hosts included *Peromyscus eremicus* (Baird) (2♀), *P. crinitis* (Merriam) (1♀ 2♂), and *Neotoma lepida* Thomas (1♀). All attachment sites were restricted to the external base of the ear pinna. Two rodents had 2 *T. monositus* each: 1 newly attached and the other a fully developed neosome. One of the 6 rodents had scarring reminiscent of a recent postneosomic infestation. Based on descriptions of the degree of engorgement during the feeding processes of *T. monositus* by Lavoipierre et al. (1979), I estimated that 2 of the fleas had been attached for less than 24 h, while the others had attained complete neosomy.

As a corollary to the presence of *T. monositus* in northern latitudes (north of 31°N to 37°N), 2 allied species (*T. caecigena* and *T. callida*) are found north of 25°N, and the former extends as far north as 33°N. All other species of *Tunga*, with exception of the widely distributed *T. penetrans*, are found at latitudes south of these. It is reported in Jordan (1962) that *T. caecigena* (China and Japan) is thought to be a univoltine species collected only during the cold season with optimal temperatures between 10° and 16°C and *T. callida* (southern China) is found only during winter months (November–March). Such evidence would suggest that *T. monositus* might also be collected in the mild, but temperate, Utah locality from October through April.

Although the 2 localities are separated by 1435 km and differ in elevation by more than 1000 m, they have similar mild, xerotic climatic conditions, desert flora, and host populations, e.g., *P. maniculatus* (Wagner), *P. eremicus*, and *Neotoma* spp. It is therefore not surprising that *T. monositus* was collected in the unique habitat and mild climate of southwestern Utah. Thorough examination for sessile fleas throughout the Southwest during the winter months may result in future collections of this peculiar flea. Perhaps it would be prudent to collect in the locality in which Wilson (1933) claims to have found "*Tunga penetrans*" among the Basket-Maker Indian ruins in Arizona.

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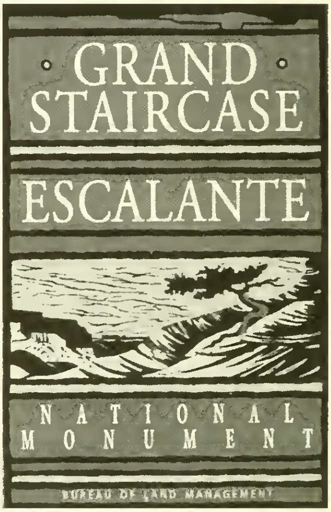

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MAYFLY FAUNA OF NEW MEXICO

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Abstract.—An inventory and analysis of the mayfly (Insecta, Ephemeroptera) fauna of New Mexico, based on the published literature and study of extensive materials from diverse collections, indicate the presence of 12 families, 37 genera, and 81 species. Of these species, 25 represent new state records: *Acentrella turbida, Ameletus falsus, A. sparsatus, Baetis adonis, B. bicaudatus, B. flavistriga, Baetodes deficiens, Caenis latipennis, Callibaetis fluctuans, Cinygmula par, Ephemera simulans, Hexagenia bilineata, Isonychia sicca, Labiobaetis propinquus, Lachlania saskatchewanensis, Leptophlebia bradleyi, Leucrocuta petersi, Neochoroterpes nanita, Paraleptophlebia debilis, P. heteronea, Procloeon conturbatum, Rhithrogena plana, R. robusta, R. vitta,* and *Thraulodes gonzalesi. Baetodes deficiens* represents a new USA record. For 37 of the 56 previously reported and confirmed species, 124 new county records are provided. With respect to continental affinities, 34 species are western, 27 southwestern, 13 widespread, 1 is a southern USA species, and 1 eastern. Of the major drainage systems in the state, the Gila system is the most species rich with 48 species, followed by the Rio Grande (46), Pecos (39), Canadian (28), and San Juan (25). Relationships between drainage systems and between New Mexico and broadly adjoining states are discussed. *Lachlania dencyannae*, the only endemic species in New Mexico, occurs in the Gila system and is rare and endangered. Certain other species from the Gila system are also noted as being at risk. From other drainages, *B. adonis, Ephemerella mollitia,* and *L. petersi* also are of some concern at the national level. Additional species that are rare in New Mexico and are of concern at least at the state level include *Ametropus albrighti, C. fluctuans, H. bilineata, L. bradleyi, N. nanita, P. conturbatum,* and *R. hageni.*

Key words: Ephemeroptera, New Mexico, species inventory.

The first report of a mayfly from New Mexico was that of *Ephemerella* sp. by Needham (1905), which was taken from the upper Pecos River in San Miguel County. This record later proved to be applicable to the common western mountain species *Drunella grandis* (Eaton). The next species was recorded when Banks (1924) described *Epeorus undulatus* [now *Rhithrogena undulata* (Banks)] from the Jemez River in Sandoval County. The discovery of additional species of mayflies in New Mexico has been mainly piecemeal. First reports of species were contributed by 21 authors since the description of *R. undulata* (Needham 1927, Traver 1935, Allen and Edmunds 1959, 1961, 1963, 1965, Peters and Edmunds 1961, Koss 1966, 1972, Allen 1968, 1978, Koss and Edmunds 1970, Kilgore and Allen 1973, Allen and Chao 1978a, 1978b, Morihara and McCafferty 1979a, Pescador and Peters 1980, Allen and Murvosh 1983, Kondratieff and Voshell 1984, Waltz and McCafferty 1987, Provonsha 1990, Henry 1993,

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Durfee and Kondratieff 1995, Lugo-Ortiz and McCafferty 1995c, Zloty 1996). Based on reports of these workers, 56 species of mayflies have been known from New Mexico prior to this study.

Six species of mayflies were described originally from New Mexico and thus have their type localities within the state. These species are *Ametropus albrighti* Traver, *Cloeodes macrolamellus* Waltz and McCafferty, *Homoeoneuria alleni* Pescador and Peters, *Lachlania dencyannae* Koss, *Rhithrogena undulata* (Banks), and *Thraulodes brunneus* Koss. Only *L. dencyannae* has proven to be endemic to New Mexico.

Our interests in the New Mexico mayfly fauna first developed in the mid-1960s when one of us (WPM) became involved in extensive collecting excursions across the state with Arwin Provonsha and Dick Koss. All of the material from those trips eventually came into the possession of WPM and Purdue University in the 1970s. Those collections and another collection made by WPM, Arwin Provonsha, and Dan Bloodgood in the early 1980s have contributed significantly to previous published revisionary studies of mayflies as well as the present study. In the late 1970s another of us (GZJ) became involved with the New Mexico Environment Department and later joined the faculty of New Mexico Highlands University. GZJ, his students, and colleagues have sampled mayflies in New Mexico for several years, often in association with various ecological studies. Another of us (CRL) developed extensive expertise on the systematics of southwestern mayflies while conducting research on the mayflies of Mesoamerica, and his familiarity with the Mexican fauna has been invaluable in the assessment of New Mexico.

The aforementioned collections of mayflies along with materials loaned or donated to us from Brigham Young University, Colorado State University, and the University of Utah have provided a large body of material upon which we have based much of the present study. We also review all published data relevant to the New Mexico mayfly fauna, provide extensive new site records for those species previously known from New Mexico, and provide new state records for an additional 25 species. We offer commentary on drainage distribution of each of the New Mexico species and synthesize all specific data and analyze the fauna as a whole with respect to faunal elements within it. Importantly, our data have served as the bases for evaluating a number of New Mexico species that can now be seen to be at environmental risk either within the state or nationally. A fine account of the history of New Mexico's hydrologic setting, beginning with the influences of the 12th-century pueblo-dwelling Native Americans, can be found in The Fishes of New Mexico by Sublette et al. (1990).

STUDY AREA

New Mexico (Fig. 1) is the 5th largest state in the USA, covering some 195,685 km^2. It possesses a diverse geologic and topographic landscape, with elevations ranging from slightly less than 1050 m at Red Bluff Reservoir in the southeastern part of the state, where the Pecos River enters Texas, to over 4550 m at Wheeler Peak in the Sangre de Cristo Mountains, approximately 50 km south of the Colorado border. Although New Mexico is the 3rd most arid state in the USA, it does receive 108,176 hectare meters of water annually either as precipitation or inflow (Harris 1984). There is significant precipitation in some higher elevations, while lower elevations are typical of deserts (see Eisenhood 1979). For example, the eastern slopes of the Sangre de Cristo Mountains and Jemez Mountains in the north central part of the state receive over 180 cm of precipitation per year, mainly as snow; Mount Taylor in the western sector, the Mogollon Mountains in the southwestern sector, and the Sacramento Mountains in the south central sector of the state receive 80–120 cm of precipitation; and southern valleys such as the Rio Grande and Tularosa receive 40 cm or less.

Five major and 3 minor drainage systems in the southwestern USA have headwaters or near-headwater flow in New Mexico. An in-depth treatment of these systems has been given by Sublette et al. (1990); however, the following brief discussion will serve the immediate purposes of this study.

The Canadian River drainage system headwaters are in the northern Sangre de Cristo Mountains. The Canadian River flows eastward through the Canadian Escarpment from the Las Vegas and Raton plateaus into the northern panhandle of Texas. In the same area of New Mexico but north of the Canadian, the Dry Cimarron River (not to be confused with

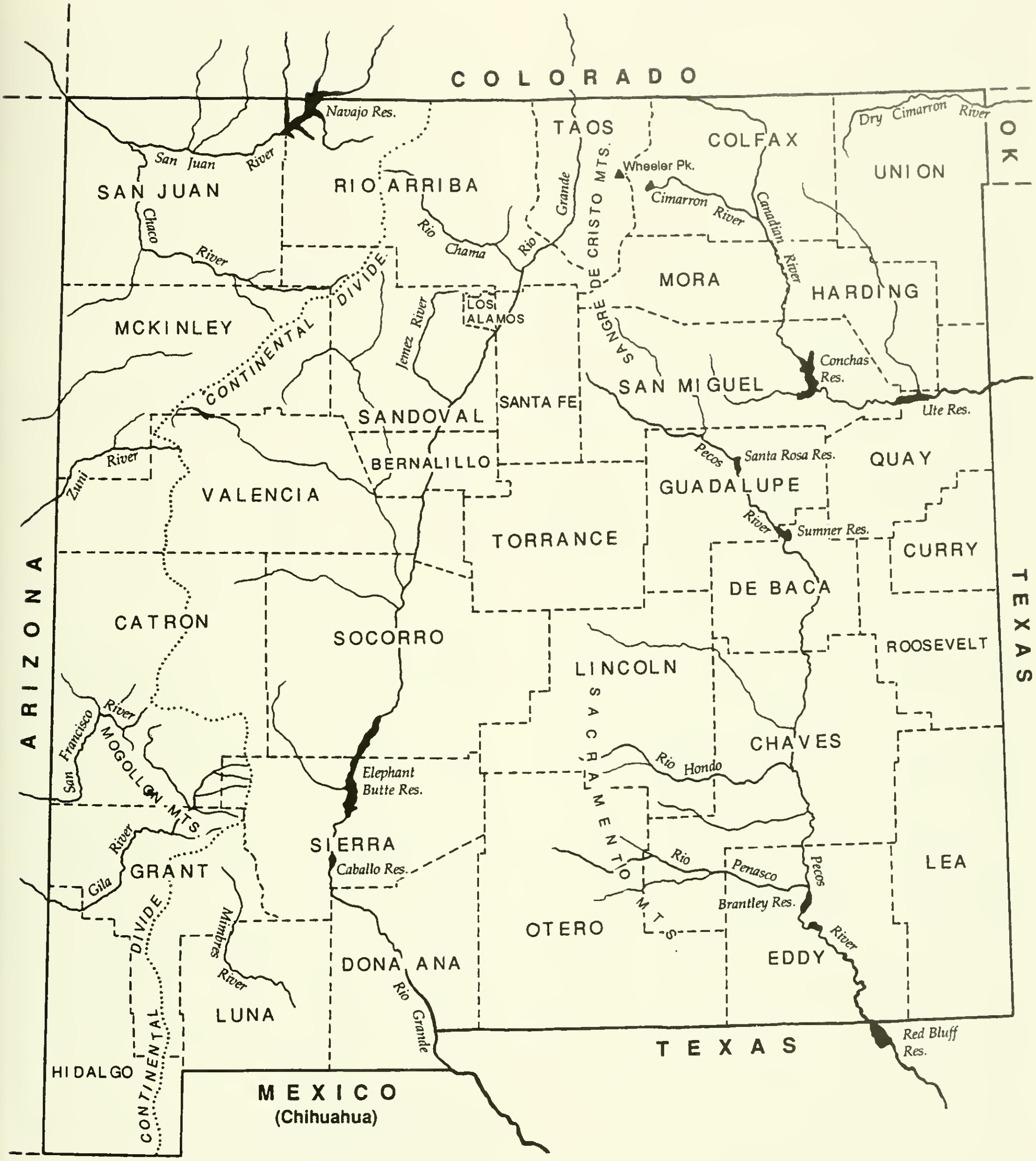
COLORADO
Navajo Res.
San Juan River
SAN JUAN
Chaco
River
RIO ARRIBA
TAOS
Rio Grande
SANGRE DE CRISTO MTS.
Wheeler Pk.
Cimarron River
COLFAX
Dry Cimarron River
OK
UNION
Canadian River
Rio Chama
Rio
MORA
HARDING
MCKINLEY
CONTINENTAL DIVIDE
LOS ALAMOS
Jemez River
SAN MIGUEL
Conchas Res.
Ute Res.
SANTA FE
SANDOVAL
BERNALILLO
Zuni River
VALENCIA
Pecos River
Santa Rosa Res.
GUADALUPE
QUAY
Sumner Res.
TORRANCE
CURRY
ARIZONA
DE BACA
TEXAS
CATRON
SOCORRO
ROOSEVELT
LINCOLN
SACRAMENTO MTS.
San Francisco River
MOGOLLON MTS.
CHAVES
Rio Hondo
Elephant Butte Res.
SIERRA
Gila River
GRANT
Caballo Res.
Rio Penasco
Pecos
LEA
Brantley Res.
Mimbres River
OTERO
River
DIVIDE
EDDY
DONA ANA
Rio Grande
LUNA
CONTINENTAL
HIDALGO
TEXAS
Red Bluff Res.
MEXICO
(Chihuahua)

Fig. 1. New Mexico, with main rivers, drainage systems, and counties indicated.

the Cimarron River in Colfax County, which is a tributary of the Canadian River within New Mexico) flows eastward off the Trinidad Escarpment and the north slope of Capulin Mountain (mainly the northern tier of Union County). These 2 river drainage systems are part of the larger Arkansas River drainage system, a major south central tributary of the Mississippi River drainage system.

Headwater streams of the Pecos River drainage originate from the southern Sangre de Cristo Mountains. The Pecos River flows southward for about 640 km through the Pecos Plains of New Mexico into west Texas, exiting New Mexico in Eddy County, and ending with its confluence with the Rio Grande at the Texas-Mexico border.

The Rio Grande, the 5th largest river in the USA, has its headwaters in south central Colorado. It flows almost directly south for over 720 km through New Mexico. The Rio Chama in Rio Arriba County is a major tributary of the Rio Grande drainage system in northern New Mexico.

Two rivers in northwestern New Mexico are part of the middle Colorado River drainage system. The 640-km-long San Juan River, with headwaters in southern Colorado, flows for about 190 km in New Mexico (mainly San Juan County) to the four corners area of Utah, Colorado, New Mexico, and Arizona, and then through extreme southeastern Utah to Lake Powell and the Colorado River. The small Zuni River, which originates in the Zuni Mountains in New Mexico south of the San Juan River, flows mainly in southern McKinley County west to the Little Colorado River in northern Arizona.

Two main rivers in southwestern New Mexico are part of the lower Colorado River drainage system. The San Francisco River drainage system originates in eastern Arizona, but a major portion of it flows in southwestern New Mexico (Catron County) before returning to Arizona, where it joins the Gila River. Headwaters of the Gila River drainage system are located near Mogollon Baldy, a peak over 3500 m high in the Mogollon Mountains. The Gila River flows for about 160 km (mainly in Grant County) to the Arizona border and continues through southern Arizona until it joins the Colorado River in the extreme southwestern corner of Arizona. The Mimbres River is also in southwestern New Mexico (Grant and Luna counties) but is internally drained.

Four physiographic divisions (provinces and plateaus) are found in New Mexico (see Snead 1979). The Canadian, Cimarron, Dry Cimarron, and Pecos rivers are found in the Great Plains Province. These rivers have dissected lava-capped plateaus and buttes and have their lower courses on broad, alluvial plains. The lower two-thirds of the Rio Grande is in the Mexican Highlands section of the Basin and Range Plateau, where upper tributaries are in isolated block-faulted mountains separated by broad plains. The upper one-third of the Rio Grande is in the Rocky Mountain Province. There, tributary streams in the Jemez and south Sangre de Cristo Mountains are separated by lava plateaus and alluvial plains. The San Juan, Zuni, San Francisco, and Gila rivers are part of the Intermontane Plateau, where landforms consist of canyon and plateaus of sedimentary or igneous rock.

METHODS AND PRESENTATION

Extensive collections of New Mexico mayflies were examined and material was identified to species whenever possible. Collections are noted in the data section with the following acronyms: BYU (Brigham Young University Collection, Provo, Utah), CSU (Colorado State University Collection, Fort Collins, Colorado), NMHU (New Mexico Highlands University Collection, Las Vegas, New Mexico), and PERC (Purdue Entomological Research Collection, West Lafayette, Indiana).

In the Species Accounts section of this work, species are presented alphabetically by family, genus, and species. Species that are newly reported for New Mexico are indicated with an asterisk. For each species, numerous data are given. First, useful descriptions of adults and larval stages of the species are referenced under the heading Descriptions. Such data are important because keys for the species are generally not available and such descriptions are part of the basis for species identification. In most cases the original description is noted and if a subsequent, more comprehensive and useful description is available, it is referenced also, as are published keys when pertinent. Historical names used in such works, if different from the current name, are also indicated so that descriptive data can be easily tracked.

If the species is newly reported for New Mexico, the complete locale data upon which the record is based are given under the heading New Records. The collection source acronym is always indicated first and if more than one collection is involved, data are presented alphabetically by collection source. If the species was a previously reported species, then the previous distributional data are given in short form under the heading Previous Records by noting only the county and body of water name and the bibliographic reference. If we have discovered additional county records, then these are given again in the same short form described above along with an indication of the collection source under the heading New County Records. Because these data are often extensive, the short form of new county records is used to conserve space. However, if the reader is interested in the entire locale information, it can be accessed from curators of the various collections indicated.

All species have a Remarks section associated with them. This generally includes a review of the overall distribution of the species, with particular attention to states surrounding New Mexico. Distribution of the species within New Mexico is also noted with respect to the drainage systems involved. Counties and drainage systems may be located using Figure 1. Other pertinent taxonomic or environmental information may also be included in the remarks.

The Faunistics section contains an analysis of the fauna in terms of its broad affinities, and inter- and intrastate relationships. Species of special note because of their rarity and environmental susceptibility are also noted here.

Species Accounts

Ameletidae

Ameletus doddsianus
Zloty, 1996

Descriptions.—Adult: Traver (1935) as *A. subnotatus* Eaton; see also Zloty (1996). Larva: Allen and Chao (1981) as *A. velox* Dodds.

Previous records.—Zloty (1996): Taos Co.

New county records.—CSU: Sierra Co (N fork Palomas Cr). NMHU: Santa Fe Co (Rio en Medio). PERC: Grant Co (Cherry Cr).

Remarks.—Zloty (1996) provided no details of his report of this species in Taos County, New Mexico; however, one of us (GZJ) has collected material of this species from the same county at a Rio Hondo (Lake Fork) beaver pond. Zloty also reported the species from Arizona, Colorado, and Utah. Certain specimens reported as *A. subnotatus* in Colorado by McCafferty et al. (1993) belong to this recently described species, and the historical confusion of what is now *A. doddsianus* and *A. subnotatus* was discussed by Zloty (1996). The occurrence of this species in New Mexico in the Gila River and upper Rio Grande drainage systems represents the southernmost part of its known range.

**Ameletus falsus*
McDunnough, 1938

Descriptions.—Adult: McDunnough (1938); see also Zloty (1996). Larva: Allen and Chao (1981) as *A.* sp. C.

New Records.—PERC: San Miguel Co, Pecos R, nr Cowles, 1-VIII-1944 (larvae); 2.2 mi N of Pecos, Pecos R, 13-VII-1969, R.W. Koss, W.P. McCafferty, and A.V. Provonsha (exuviae, larvae).

Remarks.—This species was described from Arizona by McDunnough (1938) and previous to this study has been known from only 3 counties in that state (see Zloty 1996). New Mexico specimens of *A. falsus* agree with the Allen and Chao (1981) description of *Ameletus* sp. C, and it is possible that larvae of *A.* sp. B Allen and Chao also belong to this species (Zloty 1996). *Ameletus* sp. B was reported from New Mexico by Allen and Chao (1981) from Rio Arriba County in the upper Rio Grande drainage in the Southern Rocky Mountain Province. Thus, in New Mexico, *A. falsus* apparently occurs in tributaries of the upper Rio Grande and headwaters of the Pecos River drainage system in the southern Sangre de Cristo Mountains.

**Ameletus sparsatus*
McDunnough, 1931

Descriptions.—Adult: McDunnough (1931a); see also Zloty (1996). Larva: McDunnough (1935).

New records.—NMHU: Otero Co, Agua Chiquita, nr Woods Canyon, 6-VIII-1980, G.Z. Jacobi and L. Smolka (larvae).

Remarks.—This western species was reported from Alberta, British Columbia, Colorado, Idaho, and Montana by Zloty (1996). Lugo-Ortiz and McCafferty (1995a) reported it from Arizona. Records of *A. aequivocus* McDunnough in Colorado (McCafferty et al. 1993) are also applicable to this species. In New Mexico, *A. sparsatus* has been taken only from the far southeastern part of the state in the lower Pecos River drainage system.

Ametropodidae

Ametropus albrighti
Traver, 1935

Descriptions.—Adult: Allen and Edmunds (1976). Larva: Traver (1935); see also Allen and Edmunds (1976).

Previous records.—Traver (1935): San Juan Co (San Juan R).

Remarks.—This psammophilous species was originally described from near Farmington, New Mexico, by Traver (1935). Since then it has been reported only from the Green River in southwestern Wyoming and northeastern Utah (Edmunds and Musser 1960) and the Yampa River in northeastern Colorado (Allen and Edmunds 1976), both of which are part of the upper Colorado River drainage system. In New Mexico it is known from the San Juan River drainage system in the extreme northwestern corner of the state, which is associated with the middle Colorado River drainage system. It remains to be seen if the species still exists in New Mexico.

Baetidae

Acentrella insignificans (McDunnough), 1926

DESCRIPTIONS.—Adult: McDunnough (1926) as *Baetis insignificans* McDunnough. Larva: Morihara and McCafferty (1979a) as *B. insignificans*.

PREVIOUS RECORDS.—Morihara and McCafferty (1979a) as *Baetis insignificans*: Grant Co (Gila R); Mora Co (Mora R); San Juan Co (San Juan R). Durfee and Kondratieff (1995): Catron Co (Taylor Cr).

NEW COUNTY RECORDS.—CSU: Dona Ana Co (Radium Springs). NMHU: Colfax Co (Cieneguilla Cr); Lincoln Co (Rio Ruidoso); San Miguel Co (Pecos R); Rio Arriba Co (Rio Chama); Sierra Co (Rio Grande). PERC: Catron Co (Cottonwood Cr, Gila R, Taylor Cr, Tularosa R, San Francisco R); San Miguel Co (Pecos R, Sapello R).

REMARKS.—This relatively common western species is known from all Mexican and USA states adjoining New Mexico, excluding Oklahoma (see McCafferty et al. 1993, Lugo-Ortiz and McCafferty 1995a, 1995b, McCafferty and Lugo-Ortiz 1996a). In New Mexico it is now known from throughout most of the state and all major drainage systems. It is very common in Catron County.

**Acentrella turbida* (McDunnough), 1924

DESCRIPTIONS.—Adult: McDunnough (1924a) as *Pseudocloeon turbidum* McDunnough; see also McCafferty et al. (1994). Larva: McCafferty et al. (1994).

NEW RECORDS.—NMHU: Taos Co, Costilla Cr, 17-VIII-1989, G.Z. Jacobi (larvae). PERC: San Miguel Co, Pecos R, 29-VI-1939 (larvae); 5 mi N of Pecos, Pecos R at Dalton Fishing Site, 7300 ft, 13-VII-1969, R.W. Koss, W.P. McCafferty, and A.V. Provonsha (female adults); Pecos R, 1-VIII-1936 (female adult).

REMARKS.—*Acentrella turbida* is a widespread continental species that was recently treated by McCafferty et al. (1994). It is known from all USA states bordering New Mexico (see McCafferty et al. 1993, Lugo-Ortiz and McCafferty 1995a, 1995b, McCafferty et al. 1997); however, it has not been taken in Mexico. In New Mexico, *A. turbida* has been found in the northern areas of both the Rio Grande and Pecos River drainage systems.

**Baetis adonis* Traver, 1935

DESCRIPTIONS.—Adult: Traver (1935). Larva: unknown.

NEW RECORDS.—PERC: Miguel Co, 5 mi N of Pecos, Pecos R, at Dalton Fishing Site, 7300 ft, 13-VII-1969, R.W. Koss, W.P. McCafferty, and A.V. Provonsha (male and female adults).

REMARKS.—This poorly known species is a small-sized member of the *rhodani* group that was previously known only from the San Gabriel Mountains in California (Traver 1935). Its discovery in New Mexico in the northern Pecos River drainage system therefore represents a significant range extension.

**Baetis bicaudatus* Dodds, 1923

DESCRIPTIONS.—Adult: Dodds (1923). Larva: Dodds (1923); see also Morihara and McCafferty (1979a).

NEW RECORDS.—NMHU: Mora Co, Jack's Cr, 3065 m, 18-VI-1991, M.D. Hatch (larvae). PERC: Catron Co, 42 mi N of Silver City, Rt 527 Gila R, at jct with Little Cr, 15-VII-1967, R. and D. Koss (female adult); Tularosa R, 2 mi above Aragon, 11-VI-1974, B. Stark (larvae); Lincoln Co, Sierra Blanca Ski Lodge, Rio Ruidoso, 27-VIII-1976, M.W. Sanderson (larvae); San Miguel Co., Panchuela Cr, 9-VII-1944 (larvae); Santa Fe Co, Big Tesuque Cr, Big Tesuque, 10-VI-1974, B. Stark and T.A. Wolff (larva); Little Tesuque Cr, nr Hyde Park, 2960 m, 20-IV-1973, B. Stark and T. Wolff (larva); Taos Co, Rio Trampas above El Valle, 9-VI-1974, B. Stark and T.A. Wolff (larva); Red River, 3 mi E of Questa, 9-VI-1974, B. Stark and T.A. Wolff (larvae).

REMARKS.—This relatively widespread western species is found in mountainous streams, and it reaches the southernmost limits of its range in New Mexico. Although common in Colorado (McCafferty et al. 1993), it has not been taken in Arizona, Mexico, or Texas. In New Mexico it has been collected from all major drainage systems except the San Juan

River in the extreme northwestern part of the state. With the exception of Alaska and parts of Canada, *Baetis bicaudatus* is most commonly confined to higher elevations.

Baetis caelestis
Allen and Murvosh, 1983

DESCRIPTIONS.—Adult: unknown. Larva: Morihara and McCafferty (1979a) as *B.* sp. A.

PREVIOUS RECORDS.—Morihara and McCafferty (1979a) as *Baetis* sp. A: Catron Co (San Francisco R); Otero Co (Penasco R).

NEW COUNTY RECORDS.—BYU: Grant Co (Sapillo Cr).

REMARKS.—*Baetis caelestis* is a relatively common southwestern species, presently known from Arizona (Lugo-Ortiz and McCafferty 1995a), Baja California (Allen and Murvosh 1983), Chihuahua (Lugo-Ortiz and McCafferty 1996a), and Texas (McCafferty and Davis 1992). In New Mexico, where it was originally found by Morihara and McCafferty (1979a), it is known from the Gila, lower Pecos, and San Francisco River drainage systems in the southern part of the state.

**Baetis flavistriga*
McDunnough, 1921

DESCRIPTIONS.—Adult: McDunnough (1921). Larva: Ide (1937); see also Morihara and McCafferty (1979a).

NEW RECORDS.—PERC: San Juan Co, San Juan R, river mile 165, 1820 m, 29-VI-1960 (larva).

REMARKS.—This relatively widespread North American species is known mainly from the eastern half of the continent but also from the Black Hills of South Dakota (McCafferty 1990) and several localities in Colorado (see McCafferty et al. 1993); it was recently found in the Colorado drainage area of west central Utah (McCafferty and MacDonald 1994). McCafferty and Davis (1992) reported it from Texas, and Lugo-Ortiz and McCafferty (1994) found it in the adjoining Mexican state of Chihuahua. In New Mexico, *B. flavistriga* has been taken only in the San Juan River drainage system.

Baetis magnus
McCafferty and Waltz, 1986

DESCRIPTIONS.—Adult: Durfee and Kondratieff (1993). Larva: Morihara and McCafferty (1979a) as *B.* sp. B.

PREVIOUS RECORDS.—Morihara and McCafferty (1979a) as *Baetis* sp. B: Grant Co (Cherry Cr).

NEW COUNTY RECORDS.—NMHU: Colfax Co (Canadian R); Sierra Co (Main Diamond Cr); Torrence Co (Cañón de Tajique). PERC: Catron Co (Glenwood, Gila R, Pueblo Cr); Lincoln Co (Eagle Cr, Rio Ruidoso).

REMARKS.—This western species was originally described as *Baetis* sp. B by Morihara and McCafferty (1979a), based on larvae from New Mexico, and it was later named by McCafferty and Waltz (1986). Known from western Nebraska to Panama (Lugo-Ortiz and McCafferty 1993, 1996a), it appears to be particularly common in Arizona, New Mexico, and Colorado (see also McCafferty and Waltz 1986, Durfee and Kondratieff 1993). We have recently identified larvae of this species collected by Kondratieff and Baumann in March 1993 from the San Sabo River in Menard County, southwest central Texas. *Baetis magnus* is one of the few species of mayflies now known to occur in both the Nearctic and Neotropical biogeographic regions. In New Mexico it is now known from all major drainage systems except the San Juan River (part of the middle Colorado drainage system); however, it has been taken from the Colorado drainage system in Arizona and Colorado.

Baetis notos
Allen and Murvosh, 1987

DESCRIPTIONS.—Adult: Durfee and Kondratieff (1995). Larva: Morihara and McCafferty (1979a) as *B.* sp. C.

PREVIOUS RECORDS.—Morihara and McCafferty (1979a) as *Baetis* sp. C: Catron Co (Gila R). Durfee and Kondratieff (1995): Catron Co (Taylor Cr).

NEW COUNTY RECORDS.—NMHU: Colfax Co (Cieneguilla Cr); Grant Co (Gila R, Cieneguilla Cr). PERC: Grant Co (Gila R).

REMARKS.—This southwestern species is also known from Arizona (Morihara and McCafferty 1979a), Colorado (Ward and Stanford 1990), and Texas (McCafferty and Davis 1992). It was recently discovered in Veracruz by Lugo-Ortiz and McCafferty (1994) and thus is expected to occur in northern Mexico also. Durfee and Kondratieff (1995) reared this species from Taylor Creek in Catron County, New Mexico. It has been collected in New Mexico only in the Gila, Canadian, and San Francisco River drainage systems.

Baetis tricaudatus
Dodds, 1923

DESCRIPTIONS.—Adult: Dodds (1923). Larva: Dodds (1923); see also Morihara and McCafferty (1979a).

PREVIOUS RECORDS.—Peters and Edmunds (1961) as *Baetis intermedius*: San Juan Co (San Juan R). Morihara and McCafferty (1979a): Catron Co (San Francisco R); Mora Co (Mora R); Otero Co (Rio Penasco); Rio Arriba Co (Rio Brazos); San Miguel Co (Pecos R).

NEW COUNTY RECORDS.—BYU: Grant Co (Turkey Cr, Gila R, Sapillo Cr); Lincoln Co (Rio Hondo). NMHU: Colfax Co (Canadian R, Cieneguilla Cr); Eddy Co (Rio Penasco); Grant Co (Black Canyon, Cieneguilla Cr); Guadalupe Co (Pecos R); Lincoln Co (Rio Ruidoso); Sandoval Co (Rio Cebolla, San Antonio Cr); Santa Fe Co (Rio Grande); Sierra Co (Main Diamond Cr, South Diamond Cr); Taos Co (Red R, Rio Costilla). PERC: Colfax Co (Cimarron R); Grant Co (Cherry Cr); Lincoln Co (Eagle Cr, Rio Ruidoso); Sandoval Co (Jemez R); Santa Fe Co (Rio Grande, Tesuque Cr); Taos Co (Goose Cr, La Junta Cr, Pueblo Cr, Red R, Santa Barbara R).

REMARKS.—This species is known from throughout most of North America, including Mexico (Lugo-Ortiz and McCafferty 1994), and it is probably the most widespread and ubiquitous *Baetis* on the continent. Likewise, it is now known from all major drainage systems in New Mexico.

**Baetodes deficiens*
Cohen and Allen, 1972

DESCRIPTIONS.—Adult: unknown, but subimagos were described by Flowers (1987). Larva: Cohen and Allen (1972).

NEW RECORDS.—BYU: Grant Co, Sapillo Cr, jct with Gila R, 1555 m, 26-V-1985, B. Jensen (larvae).

REMARKS.—This is essentially a Mexican species. It has been known from the Mexican states of Guerrero, Jalisco, Morelos, Sonora, and Veracruz (see McCafferty and Lugo-Ortiz 1996). Its discovery in New Mexico is important because it represents a new USA record. In New Mexico it has been taken only from the Gila River drainage system in the Intermontane Plateau.

Baetodes edmundsi
Koss, 1972

DESCRIPTIONS.—Adult: Koss (1972). Larva: Koss (1972).

PREVIOUS RECORDS.—Koss (1972): Grant Co (Gila R).

NEW COUNTY RECORDS.—NMHU: San Miguel Co (Canadian R).

REMARKS.—In addition to New Mexico, *Baetodes edmundsi* has been reported from Arizona (Koss 1972), Texas (Edmunds 1950), and the Mexican states of Sinaloa and Sonora (Allen and Murvosh 1987a). In New Mexico it has been taken only from the Gila and Canadian River drainage systems, in the far southwest and northeast regions of the state, respectively.

Callibaetis ferrugineus hageni
Eaton, 1885

DESCRIPTIONS.—Adult: Eaton (1885) as *C. hageni* Eaton. Larva: Dodds (1923) as *C. fusca* Dodds.

PREVIOUS RECORDS.—Peters and Edmunds (1961) as *Callibaetis nigritus*: San Juan Co (San Juan R).

NEW COUNTY RECORDS.—CSU: Catron Co (Wall Lake). NMHU: Taos Co (beaver pond on Rio Hondo–Lake Fork). PERC: Eddy Co (Sitting Bull Falls).

REMARKS.—This relatively widespread western subspecies ranges from Alaska southward to Arizona (Lugo-Ortiz and McCafferty 1995a) and New Mexico, and it is one of the most common mayflies in Colorado, where it was treated under the synonym *C. americanus* Banks by McCafferty et al. (1993). The extensive synonymy of the species can be found in McCafferty and Waltz (1990) and McCafferty (1996). *Callibaetis ferrugineus hageni* is not known from Texas, and therefore Arizona and New Mexico apparently represent its southeastern range limits. It has been taken in ponds and lakes in wide-ranging areas of New Mexico as well as from the San Juan River.

**Callibaetis fluctuans*
(Walsh), 1862

DESCRIPTIONS.—Adult: Walsh (1862) as *Cloe fluctuans*; see also Traver (1935). Larva: Burks (1953).

NEW RECORDS.—BYU and PERC: Eddy Co, Castle Cr, Black River Village, 14-I-1987, Baumann, Sargent, and Kondratieff (larvae).

REMARKS.—This species is known from across the continent but is most common in the Midwest. It has been taken as far west as California and Oregon in the north, but with respect to areas surrounding New Mexico, it has been reported only from Colorado (McCafferty et al. 1993) and Texas (Lugo-Ortiz and McCafferty 1995b). The isolated sample of this species from the extreme southern part of the Pecos River drainage system in New Mexico represents the southernmost limits of its western range. In southern Utah, *C. fluctuans* has historically been misidentified as *C. montanus* Eaton.

Callibaetis montanus
Eaton, 1885

DESCRIPTIONS.—Adult: Eaton (1885). Larva: Lugo-Ortiz and McCafferty (1996b).

PREVIOUS RECORDS.—Traver (1935): San Juan Co (San Juan R); Socorro Co (Rio Grande).

NEW COUNTY RECORDS.—PERC: Catron Co (Gila R), Dona Ana Co (Rio Grande).

REMARKS.—*Callibaetis montanus* has been correctly reported from Arizona and New Mexico south to Nicaragua (Eaton 1885, 1892, Banks 1900, Traver 1935, McCafferty and Lugo-Ortiz 1992). Records of the species north of Arizona and New Mexico (e.g., Edmunds 1954, Newell 1970, Rahel and Kolar 1990) are evidently misidentifications of *C. fluctuans*, and records of it in Texas are probably all or mostly attributable to *C. punctilusus* McCafferty and Provonsha (see McCafferty and Provonsha 1993, Lugo-Ortiz and McCafferty 1994). In New Mexico it has been taken from diverse areas of the Gila River, San Juan River, and Rio Grande drainage systems.

Callibaetis pictus
(Eaton), 1871

DESCRIPTIONS.—Adult: Eaton (1871) as *Baetis pictus* Eaton. Larva: Seemann (1927) as *C. pacificus* Seemann; see also Lugo-Ortiz and McCafferty (1996b).

PREVIOUS RECORDS.—Traver (1935) as *Callibaetis pacificus*: Sandoval Co (Jemez Springs). Traver (1935) as *Callibaetis signatus*: Socorro Co (Sabinal Cr).

NEW COUNTY RECORDS.—BYU: Grant Co (Turkey Cr); Rio Arriba Co (Vaceros Canyon). CSU: Sierra Co (Circle Seven Cr). PERC: Catron Co (Gila National Forest); Chaves Co (Roswell); Grant Co (Cherry Cr, Sapillo Cr, Turkey Cr, Gila R); Lincoln Co (Tucson Mts); McKinley Co (Thoreau); Sandoval Co (Galisteo Cr); San Miguel Co (Pecos R); Santa Fe Co (Galisteo Cr).

REMARKS.—This species occurs throughout western North America as far east as South Dakota (McCafferty 1990) and Texas (McCafferty and Davis 1992), and south to Costa Rica (Lugo-Ortiz and McCafferty 1996b). It is apparently one of the most common species of *Callibaetis* in New Mexico, where it has been taken in the Gila River, Pecos River, Rio Grande, and Zuni River drainage systems.

Camelobaetidius musseri
(Traver and Edmunds), 1968

DESCRIPTIONS.—Adult: unknown. Larva: Traver and Edmunds (1968) as *Dactylobaetis musseri* Traver and Edmunds; see also Lugo-Ortiz and McCafferty (1995c).

PREVIOUS RECORDS.—Lugo-Ortiz and McCafferty (1995c): Catron Co (San Francisco R, W fork Gila R, Gila R); Grant Co (E fork Gila R).

REMARKS.—This species is widespread in Mexico and Central America (Traver and Edmunds 1968, Lugo-Ortiz and McCafferty 1995c). Lugo-Ortiz and McCafferty (1995c) have recently shown that *C. salinus* Allen and Chao, which had been taken in the USA in Arizona and Nevada, is a junior synonym of *C. musseri*. In New Mexico the species appears to be restricted to the Gila and San Francisco River drainage systems in the southwestern portion of the state.

Camelobaetidius warreni
(Traver and Edmunds), 1968

DESCRIPTIONS.—Adult: Traver and Edmunds (1968) as *Dactylobaetis warreni* Traver and Edmunds. Larva: Traver and Edmunds (1968) as *D. warreni*; see also Lugo-Ortiz and McCafferty (1995c).

PREVIOUS RECORDS.—Allen and Chao (1978a) as *Dactylobaetis navis*: San Juan Co (San Juan R); as *Dactylobaetis trivialis*: Colfax Co (Cimarron R).

NEW COUNTY RECORDS.—CSU and PERC: Catron Co (W fork Gila R, Gila R, San Francisco R). NMHU: Catron Co (San Francisco R); Grant Co (E Fork Gila R).

REMARKS.—This is the most common and widespread species of *Camelobaetidius* in the western USA (known from Arizona, California, Colorado, Idaho, and Utah in addition to New Mexico), and it also ranges through Mexico (Baja California Sur, Chiapas, Chihuahua, Guerrero, Oaxaca, and Sonora) and Central America (Lugo-Ortiz and McCafferty 1995c). It has been known by many synonyms in the past as shown by Lugo-Ortiz and McCafferty (1995c), wherein *C. navis* (Allen and Chao) and *C. trivialis* (Allen and Chao), which had been reported previously from New Mexico, were synonymized with it. In New Mexico, *C. warreni* has been taken from the Canadian, Gila, San Juan, and San Francisco River drainage systems.

Cloeodes macrolamellus
Waltz and McCafferty, 1987

DESCRIPTIONS.—Adult: unknown. Larva: Waltz and McCafferty (1987).

PREVIOUS RECORDS.—Waltz and McCafferty (1987): Grant Co (Cherry Cr).

REMARKS.—*Cloeodes macrolamellus* was originally described from New Mexico by Waltz and McCafferty (1987). More recently, it was shown also to occur in the northern Mexican states of Chihuahua and Durango (Lugo-Ortiz and McCafferty 1994) and in the USA in Arizona (Lugo-Ortiz and McCafferty 1995a). In New Mexico it is known only from the Gila River drainage system.

Fallceon quilleri
(Dodds), 1923

DESCRIPTIONS.—Adult: Dodds (1923) as *Baetis quilleri* Dodds; see also Traver (1935). Larva: Morihara and McCafferty (1979a) as *B. quilleri*; see also Lugo-Ortiz et al. (1994).

PREVIOUS RECORDS.—Morihara and McCafferty (1979a) as *Baetis quilleri*: Catron Co (Gila R); Grant Co (Cherry Cr, Sapillo Cr).

NEW COUNTY RECORDS.—BYU: Eddy Co (Castle Cr). CSU: Sierra Co (Palomas Cr). PERC: Chaves Co (Rio Penasco); Dona Ana Co (small tributary of Rio Grande); Eddy Co (Castle Cr); Lincoln Co (Rio Ruidoso).

REMARKS.—This highly variable species is widespread in Central America, Mexico, and southwestern, central, and eastern USA (Lugo-Ortiz et al. 1994). In New Mexico it has thus far been taken only from the southern part of the state in the Gila River, Pecos River, and Rio Grande drainage systems. It is, however, known from the Colorado River drainage system in Colorado (McCafferty et al. 1993).

Labiobaetis apache
McCafferty and Waltz, 1995

DESCRIPTIONS.—Adult: Durfee and Kondratieff (1997). Larva: McCafferty and Waltz (1995).

PREVIOUS RECORDS.—Peters and Edmunds (1961) as *Baetis propinquus* (Walsh): San Juan Co (San Juan R).

REMARKS.—This distinctive species was recently described from the Colorado drainage system of northern Arizona and western Utah by McCafferty and Waltz (1995). We have acquired and studied the original material on which Peters and Edmunds (1961) based their record of *Baetis propinquus* (now *L. propinquus*) from the San Juan River in New Mexico, and it proved to be *L. apache*. Records of *L. propinquus* from Douglas Creek near Rangely, Colorado, in the Colorado drainage system (McCafferty et al. 1993) are also attributable to *L. apache* according to Durfee and Kondratieff (1997). The San Juan River drainage system in New Mexico is part of the middle Colorado drainage system, and thus *L. apache* remains known only from the greater Colorado drainage system in North America.

**Labiobaetis propinquus*
(Walsh), 1863

DESCRIPTIONS.—Adult: Walsh (1862) as *Cloe vicina* Walsh (nec Hagen); see also Morihara and McCafferty (1979b) as *Baetis propinquus* (Walsh). Larva: Berner (1940) as *Baetis spinosus* McDunnough; see also Morihara and McCafferty (1979b) as *B. propinquus*.

NEW RECORDS.—PERC: Colfax Co, Ponil Cr, 4.5 mi E Cimarron, 14-VII-1969, R.W. Koss, W.P. McCafferty, A.V. Provonsha (larvae); Otero Co, Rio Penasco, 12-VII-1969, R.W. Koss, W.P. McCafferty, A.V. Provonsha (larvae).

REMARKS.—This primarily central and eastern USA species evidently attains its westernmost range limits in eastern New Mexico, where we have seen it from the Canadian and Pecos River drainage systems. *Labiobaetis propinquus* was reported from Texas by McCafferty and Davis (1992) but is not known from Mexico. Published records of this species by Peters and Edmunds (1961) from the San Juan River in New Mexico are attributable to *L. apache* (see above).

**Procloeon conturbatum*
(McDunnough), 1929

DESCRIPTIONS.—Adult: McDunnough (1929) as *Centroptilum conturbatum* McDunnough;

see also Lowen and Flannagan (1991) as *C. conturbatum.* Larva: Lowen and Flannagan (1991) as *C. conturbatum.*

NEW RECORDS.—PERC: San Juan Co, San Juan R, T32N, R6W, Sec 27, river mi 165, 1820 m, 29-VI, 16-VII-1960, W.L. Peters (male adults).

REMARKS.—Specimens from the San Juan River drainage system of northeastern New Mexico agree with the redescription of this species by Lowen and Flannagan (1991). This species is known from western Canada (see Lowen and Flannagan 1991) and in the USA from California and Wyoming (Traver 1935) and Utah (Edmunds 1954). It represents a significant addition to the New Mexico mayfly fauna.

Caenidae

Caenis bajaensis
Allen and Murvosh, 1983

DESCRIPTIONS.—Adult: Provonsha (1990). Larva: Allen and Murvosh (1983); see also Provonsha (1990).

PREVIOUS RECORDS.—Provonsha (1990): Catron Co (Gila National Forest); Grant Co (Cherry Cr.).

NEW COUNTY RECORDS.—NMHU: Mora Co (Wolf Cr).

REMARKS.—*Caenis bajaensis* is also known from Arizona, Colorado, northern Mexico, and Nebraska (Provonsha 1990). Larvae of this species are apparently restricted to sandy-bottomed areas of streams with slow to moderate current. In New Mexico it is now known from the Canadian and Gila River drainage systems.

**Caenis latipennis*
Banks, 1907

DESCRIPTIONS.—Adult: Banks (1907); see also Provonsha 1990. Larva: Provonsha (1990).

NEW RECORDS.—NMHU: Eddy Co, Black R at Higby Hole, 7-VIII-1991, S.T. Pierce (larvae); Eddy Co, Delaware R above Pecos R confluence, 5-VIII-1991, G.Z. Jacobi (larvae).

REMARKS.—The range of this species extends across Canada and the USA to southern Mexico (Provonsha 1990, Lugo-Ortiz and McCafferty 1996a). With respect to areas adjacent to New Mexico, *C. latipennis* has been reported from Colorado (McCafferty et al. 1993), Oklahoma (Traver 1935), and Arizona and Texas (Provonsha 1990). Its presence in New Mexico, where it has been taken only in the lower Pecos River drainage system, was expected.

Ephemerellidae

Attenella margarita
(Needham), 1927

DESCRIPTIONS.—Adult: McDunnough (1931b) as *Ephemerella margarita* Needham. Larva: Needham (1927) as *E. margarita*; see also Allen and Edmunds (1961) as *E. margarita.*

PREVIOUS RECORDS.—Allen and Edmunds (1961) as *Ephemerella margarita*: San Miguel Co (Pecos R).

NEW COUNTY RECORDS.—NMHU: Taos Co (Costilla Cr).

REMARKS.—Western populations of this species range from British Columbia to New Mexico (Allen and Edmunds 1961, Argyle and Edmunds 1962). It has not, however, been taken from Arizona or Texas. In New Mexico it is now known from the upper Pecos River and upper Rio Grande drainage systems. This northern region in New Mexico represents the southernmost limits of the range of this species.

Drunella coloradensis
(Dodds), 1923

DESCRIPTIONS.—Adult: Dodds (1923) as *Ephemerella coloradensis* Dodds. Larva: Dodds (1923) as *E. coloradensis*; see also Allen and Edmunds (1962) as *E. coloradensis.*

PREVIOUS RECORDS.—Needham (1927) as *Ephemerella coloradensis*: San Miguel Co (Pecos R). Allen and Edmunds (1962) as *Ephemerella coloradensis*: Sandoval Co (Rock Cr); Taos Co (Santa Barbara R).

REMARKS.—This relatively common western mountain species ranges from Alaska to Arizona and New Mexico (Allen and Edmunds 1962). It apparently is restricted in New Mexico to the northern mountain regions of the Pecos River and Rio Grande drainage systems.

Drunella doddsi
(Needham), 1927

DESCRIPTIONS.—Adult: Needham (1927) as *Ephemerella doddsi* Needham. Larva: Needham (1927) as *E. doddsi*; see also Allen and Edmunds (1962) as *E. doddsi.*

PREVIOUS RECORDS.—Traver (1935) as *Ephemerella doddsi*: Santa Fe Co (Santa Fe R). Allen and Edmunds (1962) as *Ephemerella doddsi*: San Miguel Co (Pecos R).

NEW COUNTY RECORDS.—NMHU: Catron Co (Gila R); Rio Arriba Co (Rio Brazos); San Miguel Co (Gallinas R, Sapello R); Taos Co (Rio Fernando de Taos). PERC: Taos Co (Rio Hondo Canyon).

REMARKS.—New Mexico is the southernmost range limit of this common western species (Allen and Edmunds 1962). It is not known from Arizona or Texas. In New Mexico it has been taken from the Canadian River, Gila River, Pecos River, and Rio Grande drainage systems.

Drunella grandis grandis
(Eaton), 1884

DESCRIPTIONS.—Adult: Needham (1927) as *Ephemerella grandis* Eaton. Larva: Eaton (1884) as *Ephemerella, sedis incertae*, nymph #11; see also Allen and Edmunds (1962) as *E. grandis grandis*.

PREVIOUS RECORDS.—Needham (1905) as *Ephemerella* sp.?: San Miguel Co (Pecos R). Needham (1927) as *Ephemerella grandis*: Santa Fe Co (Santa Fe R). Kilgore and Allen (1973) as *Ephemerella grandis*: Lincoln Co (Rio Ruidoso).

NEW COUNTY RECORDS.—BYU: Colfax Co (Vermejo R). NMHU: Colfax Co (Cieneguilla Cr); Sierra Co (Main Diamond Cr); Taos Co (Costilla Cr, Red R). PERC: Taos Co (Rio Pueblo de Taos).

REMARKS.—This subspecies of this common western species occurs in Arizona, Colorado, New Mexico, Utah, and Wyoming (Allen and Edmunds 1962). In New Mexico it occurs in mountain tributaries mainly of the Canadian River, Pecos River, and Rio Grande drainage systems. In western drainages it is known only from Gila River drainage headwaters.

Ephemerella altana
Allen, 1968

DESCRIPTIONS.—Adult: Allen (1968). Larva: Allen (1968).

PREVIOUS RECORDS.—Allen (1968): Colfax Co (Moreno Cr); Mora Co (Mora R); San Miguel Co (Pecos R); Taos Co (Rio Grande, Rio Hondo, Rio Pueblo).

NEW COUNTY RECORDS.—PERC: Catron Co (Gila R); Grant Co (Gila R).

REMARKS.—This species has been known from Arizona and New Mexico (Allen 1968), and Lugo-Ortiz and McCafferty (1994) reported it from Baja California. In New Mexico, *E. altana* has been collected from the Canadian River, Pecos River, and Rio Grande drainage systems, and we provide the first records of it from the Gila River drainage system. In Arizona it has been collected from the middle Colorado River drainage system in the northeastern part of that state, and therefore it may eventually be found in all major drainages in New Mexico.

Ephemerella inermis
Eaton, 1884

DESCRIPTIONS.—Adult: Eaton (1884). Larva: Traver (1935); see also Allen and Edmunds (1965) and Johnson (1978).

PREVIOUS RECORDS.—Traver (1935): Sandoval Co (Jemez Springs); San Miguel Co (Pecos R). Peters and Edmunds (1961): San Juan Co (San Juan R). Allen and Edmunds (1965): Taos Co (La Junta Cr).

NEW COUNTY RECORDS.—BYU: Hondo Co (Hondo R). NMHU: Colfax Co (Cieneguilla Cr); Lincoln Co (Rio Ruidoso). PERC: Catron Co (Gila R); Colfax Co (Cimarron R); Grant Co (Gila R); Lincoln Co (Eagle Cr, Rio Ruidoso); Mora Co (Mora R); Rio Arriba Co (Rio Brazos); San Miguel Co (Pecos R).

REMARKS.—*Ephemerella inermis* is a relatively common species that occurs throughout much of western North America, excluding Mexico (Allen and Edmunds 1965). Using only the keys of Allen and Edmunds (1965), one could easily confuse specimens of the mainly eastern species *E. dorothea* Needham, which we have seen in Texas, with this strictly western species. There are, however, unpublished discriminating characters in the larvae that can be used to separate the 2 species. It is for this reason that impending records of *E. inermis* from Texas require further substantiation. In New Mexico it is known from all major drainage systems.

Ephemerella infrequens
McDunnough, 1924

DESCRIPTIONS.—Adult: McDunnough (1924b). Larva: Traver (1935); see also Allen and Edmunds (1965) and Johnson (1978).

PREVIOUS RECORDS.—Allen and Edmunds (1965): Taos Co (Red R, La Junta Cr).

REMARKS.—This western species does not occur in Arizona or Mexico, and its only records in New Mexico are from the northern part of the state in the upper Rio Grande drainage system. We have not seen material of this species from New Mexico and therefore cannot be sure that previous reports were indeed of *E. infrequens*, rather than *E. inermis*, with which it has commonly been confused in the past (see Johnson 1978).

Ephemerella mollitia
Seemann, 1927

DESCRIPTIONS.—Adult: Seemann (1927). Larva: Seemann (1927); see also Allen and Edmunds (1965).

PREVIOUS RECORDS.—Traver (1935): San Juan Co (San Juan R).

REMARKS.—This species has been known only from California and the northwestern corner of New Mexico (San Juan River drainage system). Allen and Edmunds (1965) questioned the validity of Traver's (1935) record, stating that she may have actually based the record on larvae of *E. inermis*. We have not seen the material and therefore can neither confirm nor refute the record at this time.

Serratella micheneri
(Traver), 1934

DESCRIPTIONS.—Adult: Traver (1934) as *Ephemerella micheneri* Traver. Larva: Traver (1934) as *E. micheneri*; see also Allen and Edmunds (1963) as *E. micheneri*.

PREVIOUS RECORDS.—Peters and Edmunds (1961) as *Ephemerella micheneri*: San Juan Co (San Juan R). Allen and Edmunds (1963) as *Ephemerella micheneri*: Rio Arriba Co (San Juan R). Kilgore and Allen (1973) as *Ephemerella micheneri*: Catron Co (Negrito Cr); Colfax Co (Ponil Cr); Grant Co (Little Cr).

NEW COUNTY RECORDS.—NMHU: Lincoln Co (Rio Ruidoso); Sandoval Co (Rio Cebolla); Santa Fe Co (Rio Grande).

REMARKS.—This western species is known from Arizona, Baja California, California, Colorado, New Mexico, Oregon, Washington, and Wyoming (Allen and Edmunds 1963), but it is absent from Idaho, Nevada, and Utah (essentially the Great Basin). In New Mexico it occurs in all major drainage systems.

Serratella tibialis
(McDunnough), 1924

DESCRIPTIONS.—Adult: McDunnough (1924b) as *Ephemerella tibialis* McDunnough. Larva: Walley (1930) as *E. tibialis*; see also Allen and Edmunds (1963) as *E. tibialis*.

PREVIOUS RECORDS.—Allen and Edmunds (1963) as *Ephemerella tibialis*: Taos Co (Red R).

REMARKS.—This species occurs throughout the western USA and Canada (Allen and Edmunds 1963), but it has rarely been taken in Arizona and New Mexico. In New Mexico, *S. tibialis* has been known only from the upper Rio Grande drainage system in the Rocky Mountain Province.

Timpanoga hecuba hecuba
(Eaton), 1884

DESCRIPTIONS.—Adult: McDunnough (1935) as *Ephemerella hecuba* Eaton. Larva: Eaton (1884) as *Ephemerella, sedis incertae*, nymph #4; see also Allen and Edmunds (1959) as *E. hecuba hecuba*.

PREVIOUS RECORDS.—Allen and Edmunds (1959) as *Ephemerella hecuba hecuba*: San Miguel Co (Pecos R).

NEW COUNTY RECORDS.—NMHU: Rio Arriba Co (Rio Chama).

REMARKS.—This western species, which is conspicuously absent from most of the Great Basin and Arizona (Allen and Edmunds 1959), reaches the southernmost part of its range in northern New Mexico, where it is now known from the upper Pecos River and upper Rio Grande drainage systems.

Ephemeridae

**Ephemera simulans*
Walker, 1853

DESCRIPTIONS.—Adult: Walker (1853); see also Traver (1935). Larva: Ide (1935); see also McCafferty (1975).

NEW RECORDS.—NMHU: Rio Arriba Co, Rio Chama, Hwy 84-64 bridge, 12-VI-1981, G.Z. Jacobi (female subimago).

REMARKS.—This widespread North American burrowing species was shown by McCafferty (1975) to occur from the east coast to Idaho and Utah. It is not known from Arizona, Mexico, or Texas. The new state record from the northern portion of New Mexico in the upper Rio Grande drainage system was somewhat unexpected, given the distribution pattern of this species (McCafferty 1994).

**Hexagenia bilineata*
(Say), 1824

DESCRIPTIONS.—Adult: Say (1924) as *Baetis bilineata* Say; see also Spieth (1941). Larva: Clemens (1913); see also McCafferty (1975).

NEW RECORDS.—Eddy Co, Black R, 7 mi W Malaga, 9-VII-1992, S.A. Sanders (male adult), 7-VIII-1992, S.A. Sanders, C. Gonzales, G.Z. Jacobi (larvae).

REMARKS.—The previous obscure record of this species by Spieth (1941) from the Red River, ostensibly in New Mexico, which was further recorded by McCafferty (1975), was apparently not valid. This conclusion is based on the fact that the only Red River in New Mexico is in Taos County and that stream does not have silt/marl substrate that would be required by *Hexagenia* larvae (see Keltner and McCafferty 1986). Furthermore, the material on which Spieth (1941) based his New Mexico record was from the Oklahoma Natural History Survey; and the Red River along the Oklahoma-Texas border in the eastern parts of those states does possess substrate types required by *Hexagenia* larvae. Nonetheless, we do provide the first valid record of this species in New Mexico. The male adult from Eddy County, New Mexico (lower Pecos River drainage system), clearly possesses the beaklike penes typical of *H. bilineata*; however, both the larvae and adult are very lightly pigmented, which is atypical of *H. bilineata*. Although *H. bilineata* is known from Texas and Oklahoma, it has not been found north, west, or south of New Mexico, with the exception of a record from the Mexican state of San Luis Potosí by McCafferty (1968). The most widespread species of *Hexagenia* in North America, *H. limbata* (Serville), has not been found in New Mexico but may eventually because it does occur in Colorado and Texas.

Heptageniidae

**Cinygmula par*
(Eaton), 1885

DESCRIPTIONS.—Adult: Eaton (1885) as *Cinygma par* Eaton. Larva: not published.

NEW RECORDS.—NMHU: San Miguel Co, Elk Mtn (elev. 3540 m), below springs, VII-1980, L.R. Smolka (male and female adults).

REMARKS.—This species occurs in the higher elevations throughout much of western North America, including Arizona (Eaton 1885) and Colorado (Dodds 1923). It is not known from Mexico or Texas. In New Mexico, *C. par* is the only species of the genus thus far taken, and it has been found only in mountain headwaters of the Pecos River.

Epeorus albertae
(McDunnough), 1924

DESCRIPTIONS.—Adult: McDunnough (1924a) as *Iron albertae* McDunnough. Larva: Edmunds and Allen (1964).

PREVIOUS RECORDS.—Allen and Chao (1978b): Rio Arriba Co (Rio Chama).

REMARKS.—Ward and Berner (1980) indicated that this western species tended to replace other species of *Epeorus* at lower elevations. *Epeorus albertae* is relatively common in Colorado (McCafferty et al. 1993), but it has not been taken in Arizona, Mexico, or Texas. In New Mexico it has been taken only in the northern part of the state in the upper Rio Grande drainage system.

Epeorus deceptivus
(McDunnough), 1924

DESCRIPTIONS.—Adult: McDunnough (1924a) as *Iron deceptivus* McDunnough. Larva: Edmunds and Allen (1964).

PREVIOUS RECORDS.—Allen and Chao (1978b): San Miguel Co (Pecos R).

NEW COUNTY RECORDS.—NMHU: Sierra Co (South Diamond Cr). PERC: Taos Co (Rio Hondo).

REMARKS.—Edmunds and Allen (1964) indicated that this species was confined to the intermountain western USA, and those authors were the first to indicate its occurrence in New Mexico, but they did not provide any specific locale data. Allen and Chao (1978b) recorded it from Gila County, Arizona. In New Mexico we know of this species from the upper Pecos River and upper Rio Grande drainage systems, as well as the Gila River drainage system in the southwestern part of the state.

Epeorus longimanus
(Eaton), 1885

DESCRIPTIONS.—Adult: Eaton (1885) as *Iron longimanus* Eaton. Larva: Dodds (1923) as *Iron* nymph #1; see also Edmunds and Allen (1964).

PREVIOUS RECORDS.—Allen and Chao (1978b): Rio Arriba Co (Canjilon Cr); San Miguel Co (Pecos R, Winsor Cr); Taos Co (Red R, Rio Pueblo, Rio Chiquito). Durfee and Kondratieff (1995): Catron Co (Taylor Cr).

NEW COUNTY RECORDS.—NMHU: Lincoln Co (Rio Ruidoso). PERC: Lincoln Co (Eagle Cr).

REMARKS.—*Epeorus longimanus* is the most widespread of the western species of *Epeorus*

(Edmunds and Allen 1964). It is very common at higher elevations in Colorado and Utah, but somewhat less common in Arizona and New Mexico. In New Mexico it has been taken from the Gila River, upper Pecos River, and upper Rio Grande drainage systems.

Epeorus margarita
Edmunds and Allen, 1964

DESCRIPTIONS.—Adult: Edmunds and Allen (1964). Larva: Edmunds and Allen (1964).

PREVIOUS RECORDS.—Durfee and Kondratieff (1995): Catron Co (Taylor Cr).

NEW COUNTY RECORDS.—PERC: Grant Co (Gila R); Rio Arriba Co (Rio Brazos).

REMARKS.—We have numerous samples of *Epeorus margarita* from Catron County collected in the 1960s and 1980s. The species is by far the most common species of *Epeorus* found in the Gila River drainage system, and except for the Rio Brazos, a headwater stream in the upper Rio Grande drainage system, it has not been taken from the other major drainage systems in the state. *Epeorus margarita* was recently reported from numerous localities in the Mexican state of Chihuahua by Lugo-Ortiz and McCafferty (1996a), and the species has been known from a few localities in Arizona (Edmunds and Allen 1964) and Baja California (Allen and Murvosh 1983).

Heptagenia elegantula
(Eaton), 1885

DESCRIPTIONS.—Adult: Eaton (1885) as *Rhithrogena elegantula* Eaton. Larva: Needham and Christenson (1927) as *R. elegantula*; see also Bednarik and Edmunds (1980).

PREVIOUS RECORDS.—Peters and Edmunds (1961): San Juan Co (San Juan R). Allen and Chao (1978b): Colfax Co (Cimarron R, Ponil Cr).

REMARKS.—This species is known from throughout much of western North America, including Arizona and Colorado (Eaton 1885) and Utah (Edmunds 1954). It has not been found in Mexico, Oklahoma, or Texas. Larvae of *Heptagenia elegantula* can be distinguished from the somewhat similar *H. solitaria* (see below) with the use of the key by Bednarik and Edmunds (1980). The species prefers silted streams at lower elevations, and in New Mexico it is known only from the Canadian and San Juan River drainage systems in the northern part of the state.

Heptagenia solitaria
McDunnough, 1924

DESCRIPTIONS.—Adult: McDunnough (1924a). Larva: Bednarik and Edmunds (1980).

PREVIOUS RECORDS.—Peters and Edmunds (1961): San Juan Co (San Juan R).

NEW COUNTY RECORDS.—PERC: Catron Co (Gila R); Colfax Co (Canadian R, Cimarron R); Grant Co (Gila R); Mora Co (Coyote Cr); Sandoval Co (Rio Grande).

REMARKS.—McCafferty et al. (1993) noted that in Colorado this western species was found primarily on the western slope of the Colorado Plateau. It is one of the most common species of *Heptagenia* in the West and has also been found in the Gila River and middle Colorado drainage systems in Arizona (Lugo-Ortiz and McCafferty 1995a). It is not known from Mexico or Texas. In New Mexico it has been taken in the Canadian River, Gila River, Rio Grande, and San Juan River drainage systems.

**Leucrocuta petersi*
(Allen), 1966

DESCRIPTIONS.—Adult: Allen (1966) as *Heptagenia petersi* Allen. Larva: Bednarik and Edmunds (1980) as *H. petersi*.

NEW RECORDS.—NMHU: Colfax Co, Sixmile Cr, nr Hwy 64, 2530 m, 9-IX-93, G.Z. Jacobi (larvae). PERC: Catron Co, 2 mi N Silver City, Rt 527, Gila R at jct with Little Cr, 15-VII-1967, R. and D. Koss (female adults); Gila Cliff Dwellings National Monument, Gila R at jct with Little Cr, 15-VII-1967, R. and D. Koss (male and female adults); N Silver City, middle fork Gila R, .25 mi above jct with W fork, 9-VII-1969, R.W. Koss, W.P. McCafferty, and A.V. Provonsha (female adult); Grant Co, 65 km N Silver City, Rt 527, E fork Gila R, 15-16-VII-1967, R. and D. Koss (larva).

REMARKS.—This species was previously known only from the Green River (upper Colorado Drainage) in southwestern Wyoming and northeastern Utah (Allen 1966). New records from New Mexico are therefore significant. In New Mexico, *L. petersi* has been taken in the Canadian and Gila River drainage systems. It is possible that this species presently occurs only in New Mexico because of its possible extirpation in Utah and Wyoming.

Nixe criddlei
(McDunnough), 1927

DESCRIPTIONS.—Adult: McDunnough (1927)

as *Heptagenia criddlei* McDunnough. Larva: Bednarik and Edmunds (1980) as *H. criddlei.*

PREVIOUS RECORDS.—Peters and Edmunds (1961) as *Heptagenia* sp.: San Juan Co (San Juan R). Allen and Chao (1978b) as *Heptagenia criddlei*: Catron Co (San Francisco R); Colfax Co (Cimarron R, Moreno Cr); Grant Co (Sapillo Cr); Lincoln Co (Bonito Cr, Cr at Pine Lodge); Mora Co (Mora R); Rio Arriba Co (Wolf Cr); Taos Co (Rio Hondo); Valencia Co (Blue Water Cr).

NEW COUNTY RECORDS.—CSU: Sierra Co (Palomas Cr). PERC: Sandoval Co (Jemez R); San Miguel Co (Pecos R).

REMARKS.—This relatively common species is known from throughout the western USA (McDunnough 1927, Traver 1935, Edmunds 1954, Peters and Edmunds 1961, Allen and Chao 1978b). *Nixe criddlei* has been taken from all major drainage systems within New Mexico.

Nixe simplicioides
(McDunnough), 1924

DESCRIPTIONS.—Adult: McDunnough (1924a) as *Heptagenia simplicioides* McDunnough. Larva: Bednarik and Edmunds (1980) as *H. simplicioides.*

PREVIOUS RECORDS.—Peters and Edmunds (1961) as *Heptagenia simplicioides*: San Juan Co (San Juan R).

NEW COUNTY RECORDS.—BYU: Grant Co (Gila R, Turkey Cr); Sandoval Co (Jemez R). NMHU: Rio Arriba Co (Rio Chama). PERC: Catron Co (Gila R); Lincoln Co (Bonito Cr); Mora Co (Coyote Cr); San Miguel Co (Pecos R).

REMARKS.—This species is known from the western USA (Traver 1935, Edmunds 1954, Peters and Edmunds 1961, Allen and Chao 1978b, Bednarik and Edmunds 1980) and Alberta (McDunnough 1924a). Previously, it was known from New Mexico only from the San Juan River drainage system in the northwest corner of the state. We report it from all major drainage systems in New Mexico.

Rhithrogena hageni
Eaton, 1885

DESCRIPTIONS.—Adult: Eaton (1885). Larva: not described, but keyed by Day (1963).

PREVIOUS RECORDS.—Allen and Chao (1978b): Taos Co (Red R).

REMARKS.—This western USA species is also known from Colorado (Dodds 1923) and Utah (Needham and Christenson 1927), and it is relatively common in southern areas of Colorado (e.g., McCafferty et al. 1993). In Arizona and New Mexico, *R. hageni* is known from only a single locality in each state (Allen and Chao 1978b). In New Mexico it is known from the upper Rio Grande drainage system.

Rhithrogena morrisoni
(Banks), 1924

DESCRIPTIONS.—Adult: Banks (1924) as *Epeorus morrisoni* Banks; see also Traver 1935. Larva: Seemann (1927) as *Iron petulans* Seemann; see also key by Allen and Chao (1978b).

PREVIOUS RECORDS.—Allen and Chao (1978b): Colfax Co (Cimarron R); San Miguel Co (Pecos R); Taos Co (Red R, Rio Chiquito).

NEW COUNTY RECORDS.—NMHU: San Juan Co (San Juan R).

REMARKS.—This species is known from much of the West, from Alberta (McDunnough 1934) to Baja California in northern Mexico (Lugo-Ortiz and McCafferty 1994). With respect to the states adjacent to New Mexico, it is known only from Arizona (see Lugo-Ortiz and McCafferty 1995a). Although McCafferty et al. (1993) did not record *R. morrisoni* from Colorado, they noted that materials commonly identified as *R. undulata* (Banks) in Colorado and elsewhere were probably referable to this species. In New Mexico it has been taken in the northern part of the state, in the Canadian River, Pecos River, Rio Grande, and San Juan River drainage systems.

**Rhithrogena plana*
Allen and Chao, 1978

DESCRIPTIONS.—Adult: unknown. Larva: Allen and Chao (1978b).

NEW RECORDS.—PERC: Grant Co, Duck Cr at Cliff, US 180, 5-V-1981, W.P. McCafferty, A.V. Provonsha, and D. Bloodgood (larva); Gila R at US 180, nr Cliff, 5-V-1981, W.P. McCafferty, A.V. Provonsha, and D. Bloodgood (larva); Taos Co, S fork of Red R, Carson National Forest, 27-VII-1937, C. Tarzwell (larvae).

REMARKS.—This species was previously known only from Arizona (Allen and Chao 1978b), where it was described from the White River in Navajo County. We report it for the first time from New Mexico from the Gila River and Rio Grande drainage systems. McCafferty et al. (1993) indicated that *R. plana* may eventually prove to be a variant of *R. morrisoni.*

**Rhithrogena robusta*
Dodds, 1923

DESCRIPTIONS.—Adult: Dodds (1923). Larva: Dodds (1923); see also key by Allen and Chao (1978b).

NEW RECORDS.—NMHU: Santa Fe Co, Rio En Medio, 2990 m, 13-V-1992, G.Z. Jacobi (larvae). PERC: Grant Co, 1 mi S Cliff, tributary to Gila R, 14-VII-1967, R. and D. Koss (larvae); Taos Co, creek in Hondo Canyon, nr Taos Ski Valley, 22-III-1967, R.W. Baumann (larvae).

REMARKS.—The new New Mexico state records of the distinctive *R. robusta* represent the southernmost limits of the known range of this boreal western species. In New Mexico it has been taken in the Gila River and upper Rio Grande drainage systems. It co-occurs with *R. plana* in Grant County, where the species are distinct from each other. Cohabitation by *Rhithrogena* species is often common (Leonard and Leonard 1962, McCafferty et al. 1997).

Rhithrogena undulata
(Banks), 1924

DESCRIPTIONS.—Adult: Banks (1924) as *Epeorus undulatus* Banks. Larva: not published, but keyed by Flowers and Hilsenhoff (1975) and Allen and Chao (1978b).

PREVIOUS RECORDS.—Banks (1924) as *Epeorus undulatus*: Sandoval Co (Jemez R). Peters and Edmunds (1961): San Juan Co (San Juan R). Allen and Chao (1978b): Colfax Co (Cimarron R); San Miguel Co (Pecos R); Taos Co (Red R).

NEW COUNTY RECORDS.—NMHU: Rio Arriba Co (Rio Chama). PERC: Grant Co (Gila R); Rio Arriba Co (Rio Brazos).

REMARKS.—*Rhithrogena undulata* is a western and central North American species, but it was originally described from New Mexico (Banks 1924). With respect to states adjacent to New Mexico, the species has been reported from Arizona (Allen and Chao 1978b) and Colorado (Peters and Edmunds 1961), but it is not known from Mexico, Oklahoma, or Texas. McCafferty et al. (1993) indicated that this species was confined to the western slope of the Colorado Plateau, and Lugo-Ortiz and McCafferty (1995a) indicated that in Arizona it was restricted to the Colorado River drainage system. However, it is not confined to the San Juan River drainage system (middle Colorado River drainage system) in New Mexico but is relatively widespread, being found in all main drainage systems.

**Rhithrogena vitta*
Allen and Chao, 1978

DESCRIPTIONS.—Adult: unknown. Larva: Allen and Chao (1978b).

NEW RECORDS.—BYU: Grant Co, Gila R, above mouth Turkey Cr, 1455 m, 27-V-1985, B. Jensen (larvae). PERC: Grant Co, E fork of Gila R at Rd 15, Gila National Forest, 6-V-1981, W.P. McCafferty, A.V. Provonsha, and D. Bloodgood (larvae).

REMARKS.—This species was previously known only from Arizona, where it was described from the White River in Apache and Navajo counties (middle Colorado drainage system) by Allen and Chao (1978b). In New Mexico we found it in the southwestern portion of the state in the Gila River drainage system (also a part of the greater Colorado River drainage system).

Isonychiidae

Isonychia intermedia
(Eaton), 1885

DESCRIPTIONS.—Adult: Eaton (1885) as *Chirotonetes intermedius* Eaton. Larva: Kondratieff and Voshell (1984).

PREVIOUS RECORDS.—Kondratieff and Voshell (1984): Catron Co (San Francisco R); Dona Ana Co (Rio Grande); Grant Co (Gila R).

NEW COUNTY RECORDS.—NMHU: Socorro Co (Rio Grande).

REMARKS.—*Isonychia intermedia* is known from several localities in Arizona and Chihuahua (Kondratieff and Voshell 1984, Lugo-Ortiz and McCafferty 1995a), in addition to those localities in New Mexico noted above. In New Mexico it has been taken from the Gila River, Rio Grande, and San Francisco River drainage systems in the southern part of the state. We do not expect it to be found in either the Rocky Mountain or Great Plains provinces.

**Isonychia sicca*
(Walsh), 1862

DESCRIPTIONS.—Adult: Walsh (1862) as *Baetis sicca* Walsh; see also Kondratieff and Voshell (1984). Larva: Allen and Cohen (1977) as *I. sicca manca* (Eaton); see also Provonsha and McCafferty (1982).

NEW RECORDS.—BYU: Sandoval Co, Rio Grande, Coronado State Park, Bernalillo, 21-VIII-1985, Baumann and Whiting (larvae).

REMARKS.—*Isonychia sicca* is a relatively widespread species in North America (Kondratieff and Voshell 1984), being especially common in the Midwest, but extending to Central America. With respect to areas adjacent to New Mexico, it is common in Texas (Lugo-Ortiz and McCafferty 1995b), but has also been reported from Chihuahua (Lugo-Ortiz and McCafferty 1996a) and Oklahoma (McCafferty et al. 1997). Its discovery in New Mexico, where it is thus far known only from the Rio Grande drainage system, is somewhat expected. Larvae of *I. sicca* and *I. campestris* McDunnough, of which the latter occurs in Alberta, Saskatchewan, Wyoming, northeast Utah, and northwest Colorado (Woodbury and Argyle 1963), cannot be distinguished confidently (Kondratieff and Voshell 1984). Therefore, although there is the possibility that larvae we have seen belong to *I. campestris*, the Sandoval County record would appear more consistent geographically with the range of *I. sicca*. Also, the *I. sicca* identification is more consistent with larvae taken from the Rio Grande. Yanoviak and McCafferty (1995) showed that *I. sicca* is typically found in very long stream regions (>200 km), whereas *I. campestris* is known only from stream regions 100–200 km in length.

Leptohyphidae

Leptohyphes apache
Allen, 1967

DESCRIPTIONS.—Adult: unknown. Larva: Allen (1967).

PREVIOUS RECORDS.—Allen (1967): Rio Arriba Co (Taylor Cr). Allen (1978): Catron Co (San Francisco R); Grant Co (Gila R).

REMARKS.—This southwestern species is known from Arizona and southern Utah (Allen 1967, 1978, Lugo-Ortiz and McCafferty 1995a) and Chihuahua (Lugo-Ortiz and McCafferty 1994), in addition to New Mexico. In New Mexico, *L. apache* is known only from the Intermontane Plateau in the western part of the state, including the Gila, San Francisco, and San Juan River drainage systems.

Tricorythodes condylus
Allen, 1967

DESCRIPTIONS.—Adult: Allen (1967). Larva: Allen (1967).

PREVIOUS RECORDS.—Kilgore and Allen (1973): Catron Co (Gila R); Grant Co (Sapillo Cr).

REMARKS.—*Tricorythodes condylus* is a southwestern species known from Arizona, Chihuahua, New Mexico, and Sonora (Allen 1967, Kilgore and Allen 1973, Lugo-Ortiz and McCafferty 1994). In New Mexico it is known only from the Gila River drainage system.

Tricorythodes corpulentus
Kilgore and Allen, 1973

DESCRIPTIONS.—Adult: unknown. Larva: Kilgore and Allen (1973).

PREVIOUS RECORDS.—Kilgore and Allen (1973): Catron Co (Gila R).

REMARKS.—This species is known only from the Gunnison River in Colorado (Ward and Stanford 1990) and Gila River in New Mexico. McCafferty et al. (1993) pointed out that *T. corpulentus* was only tentatively valid. We have not seen specimens of this species.

Tricorythodes dimorphus
Allen, 1967

DESCRIPTIONS.—Adult: Kilgore and Allen (1973). Larva: Allen (1967).

PREVIOUS RECORDS.—Allen (1967): Taos Co (Red R). Kilgore and Allen (1973): Catron Co (N Glenwood); Grant Co (Sapillo Cr); Sierra Co (Rio Grande).

REMARKS.—This southwestern species is known from Arizona (Allen 1967, Kilgore and Allen 1973, Gray 1981, Lugo-Ortiz and McCafferty 1995a), Chihuahua, and New Mexico (Lugo-Ortiz and McCafferty 1994). In New Mexico it has been taken from the Gila and Rio Grande drainage systems.

Tricorythodes explicatus
(Eaton), 1892

DESCRIPTIONS.—Adult: Eaton (1892) as *Tricorythus explicatus* Eaton. Larva: Allen and Murvosh (1987c).

PREVIOUS RECORDS.—Allen and Murvosh (1983): Dona Ana Co (trib Rio Grande).

NEW COUNTY RECORDS.—NMHU: Colfax Co (Cieneguilla Cr, Six-mile Cr); Eddy Co (Penasco R); Lincoln Co (Rio Ruidoso); Rio Arriba Co (Rio Chama); Sierra Co (Rio Grande). PERC: San Juan Co (San Juan R).

REMARKS.—This species is known from Arizona and throughout northern Mexico (see Lugo-Ortiz and McCafferty 1995a, McCafferty and Lugo-Ortiz 1996). In New Mexico, *T. explicatus* is relatively common and is now known from the Canadian River, Pecos River, Rio Grande, and San Juan River drainage systems. Lugo-Ortiz and McCafferty (1995a) indicated some possibility that *T. explicatus* and *T. minutus* Traver were synonymous.

Tricorythodes minutus
Traver, 1935

DESCRIPTIONS.—Adult: Traver (1935). Larva: Kilgore and Allen (1973).

PREVIOUS RECORDS.—Kilgore and Allen (1973): Catron Co (San Francisco R); Chaves Co (Rio Penasco); Colfax Co (Ponil Cr); Grant Co (Gila R); Lincoln Co (Rio Ruidoso); Mora Co (Mora R); Rio Arriba Co (Rio Chama); Sandoval Co (Jemez R); San Juan Co (San Juan R); Sierra Co (Rio Grande); San Miguel Co (Sapello Cr); Santa Fe Co (Rio Grande); Taos Co (Taos Cr).

REMARKS.—*Tricorythodes minutus* is apparently widespread and ubiquitous in much of Canada and the USA. It has not been found in Mexico or Texas. It was reported as common throughout much of Colorado by McCafferty et al. (1993). In New Mexico, Kilgore and Allen (1973) have reported it from all major drainage systems, although we have not seen any material of this species from the many collections we have examined. Lugo-Ortiz and McCafferty (1995a) indicated that *T. minutus* could be easily confused with *T. explicatus* (see above).

Leptophlebiidae

Choroterpes inornata
Eaton, 1892

DESCRIPTIONS.—Adult: Eaton (1892). Larva: Kilgore and Allen (1973).

PREVIOUS RECORDS.—Kilgore and Allen (1973): Catron Co (San Francisco R); Colfax Co (Cimarron R); Grant Co (Sapillo Cr); San Miguel Co (Windsor Cr).

NEW COUNTY RECORDS.—NMHU: Sandoval Co (Rio Cebolla). PERC: Mora Co (Coyote Cr).

REMARKS.—In addition to New Mexico, the southwestern species *C. inornata* is known from Arizona and northern Mexico (Eaton 1892), including Chihuahua (Allen and Murvosh 1987b), Colorado (Ward and Berner 1980), and more recently in Texas (Lugo-Ortiz and McCafferty 1995b) and Utah (McCafferty and MacDonald 1994). In New Mexico, *C. inornata* is now known from all major drainage systems except the San Juan River drainage system. Since it is found in the greater Colorado River drainage system in Arizona, Colorado, and Utah, it could eventually also be found in that drainage system in New Mexico.

**Leptophlebia bradleyi*
Needham, 1932

DESCRIPTIONS.—Adult: Needham (1932). Larva: Berner (1975).

NEW RECORDS.—CSU: Eddy Co, Sitting Bull Falls, 16-I-1993, S. Fitzgerald and S. Hoffman (larvae, male adults).

REMARKS.—This species is known from the southeastern USA and Texas (Henry and Kondratieff 1982). Here we report it from New Mexico near Texas in the lower Pecos River drainage system. The New Mexico record represents the westernmost limits of its presently known range.

Neochoroterpes kossi
(Allen), 1974

DESCRIPTIONS.—Adult: Henry (1993). Larva: Allen (1974) as *Choroterpes kossi* Allen; see also Henry (1993).

PREVIOUS RECORDS.—Henry (1993): Catron Co (San Francisco R).

NEW COUNTY RECORDS.—PERC: Grant Co (Cherry Cr, Little Cr).

REMARKS.—In addition to New Mexico, *N. kossi* has been known from Arizona (Allen 1974), from where it was originally described, and Texas (Henry 1993). Previous and new records from New Mexico are confined to the Gila River drainage system.

**Neochoroterpes nanita*
(Traver), 1934

DESCRIPTIONS.—Adult: Traver (1934) as *Choroterpes nanita* Traver; see also Henry (1993). Larva: Allen (1974) as *C. nanita*; see also Henry (1993).

NEW RECORDS.—NMHU: San Miguel Co, Canadian R at Sanchez, 21-III-1988, L.R. Smolka (larvae).

REMARKS.—This species was previously known only from Texas (Traver 1934). In New Mexico it has been taken in the Canadian River drainage system, which continues east into Texas.

Neochoroterpes oklahoma
(Traver), 1934

DESCRIPTIONS.—Adult: Traver (1934) as *Choroterpes oklahoma* Traver; see also Henry

(1993). Larva: Allen (1974) as *C. mexicanus* Allen; see also Henry (1993).

PREVIOUS RECORDS.—Henry (1993): Chaves Co (Rio Penasco); Eddy Co (Sitting Bull Falls).

NEW COUNTY RECORDS.—CSU: Colfax Co (Vermejo R). NMHU: Otero Co (Dog Canyon). PERC: Mora Co (Coyote Cr).

REMARKS.—This species, which has been known more commonly by the synonyms *Choroterpes mexicanus* Allen or *Neochoroterpes mexicana* (Allen) (see McCafferty et al. 1993 and Henry 1993), is known from Colorado, parts of Mexico (including Chihuahua), Oklahoma, and Texas (see Henry 1993, McCafferty et al. 1993, Lugo-Ortiz and McCafferty 1996a). In New Mexico this species is now known from the eastern part of the state in both the Canadian and Pecos River drainage systems.

**Paraleptophlebia debilis*
(Walker), 1853

DESCRIPTIONS.—Adult: Walker 1853 as *Baetis debilis* Walker; see also key of Harper and Harper (1986). Larva: Ide (1930) as *Leptophlebia debilis*.

NEW RECORDS.—BYU: Eddy Co, Castle Cr, Black River Village, 14-I-1987, Baumann, Sargent, and Kondratieff (larvae). PERC: Grant Co, N of Silver City, Cherry Cr, 2.4 mi N of Cherry Creek Campgrounds, 7-VII-1969, R.W. Koss, W.P. McCafferty, and A.V. Provonsha (larvae); Sandoval Co, ca 32 km W of Los Alamos, Santa Fe National Forest, Las Conchas Picnic Site, E fork Jemez R, 1-IX-1969, R. and D. Koss; San Miguel Co, 1 mi N of Pecos, Pecos R, just below Lisboa Springs Fish Hatchery, 31-VIII-1969, R. and D. Koss (larvae).

REMARKS.—This transcontinental species is known from Colorado (Ward and Stanford 1990) and Utah (Edmunds 1954) but no other states adjoining New Mexico. Its presence in New Mexico therefore appears to represent the southernmost range limits in western North America. In New Mexico, *P. debilis* is presently known from all major drainage systems with the exception of the San Francisco and San Juan River drainage systems.

**Paraleptophlebia heteronea*
(McDunnough), 1924

DESCRIPTIONS.—Adult: McDunnough (1924a) as *Leptophlebia heteronea* McDunnough; see also key of Harper and Harper (1986). Larva: not published.

NEW RECORDS.—NMHU: Mora Co, Jack's Cr, 10,650 ft, 18-VI-1991, M. Hatch (larvae); Rio Arriba Co, San Pedro Park, south entrance, 13-VI-1981, S. Cary (male and female adults).

REMARKS.—McDunnough (1924a) first described *Paraleptophlebia heteronea* from Alberta. The species was misidentified from Colorado as *Leptophlebia pallipes* Hagen [now *P. memorialis*, see below] by Dodds (1923) and was similarly misidentified from Utah somewhat later by Needham and Christenson (1927). However, it was correctly reported from those states by Ward and Berner (1980) and Edmunds (1954), respectively. Our new records of this species in New Mexico are based on both the more identifiable adults as well as larvae. In New Mexico it has been taken in the northern part of the state in the Canadian River and Rio Grande drainage systems.

Paraleptophlebia memorialis
(Eaton), 1884

DESCRIPTIONS.—Adult: Eaton (1884) as *Leptophlebia memorialis* Eaton; see also key of Harper and Harper (1986). Larva: Seemann (1927) as *Leptophlebia rufivenosa* Eaton 1884; see also Kilgore and Allen (1973).

PREVIOUS RECORDS.—Peters and Edmunds (1961) as *Paraleptophlebia pallipes*: San Juan Co (San Juan R). Kilgore and Allen (1973): Catron Co (Whitewater R); Lincoln Co (Cr at Pine Lodge).

NEW COUNTY RECORDS.—BYU: Sandoval Co (Jemez R). PERC: Colfax Co (Cimarron R); San Miguel Co (Pecos R); Rio Arriba Co (Rio Brazos); Taos Co (Pueblo Cr).

REMARKS.—This common western species is known from all USA states adjacent to New Mexico, except Oklahoma and Texas (Edmunds 1954, Argyle and Edmunds 1962, Kilgore and Allen 1973). *Paraleptophlebia memorialis* has often been recorded under its junior synonym *Leptophlebia pallipes* Hagen, which proved to be an unavailable name because it was a homonym of *L. pallipes* (Walker), 1875. *Paraleptophlebia memorialis* has been taken in Mexico only in Baja California (Lugo-Ortiz and McCafferty 1994). In New Mexico it is now known from all major drainage systems.

Thraulodes brunneus
Koss, 1966

DESCRIPTIONS.—Adult: Koss (1966). Larva: Kilgore and Allen (1973).

PREVIOUS RECORDS.—Koss (1966): Grant Co (N Silver City).

NEW COUNTY RECORDS.—PERC: Catron Co (Gila R).

REMARKS.—*Thraulodes brunneus* is known from Arizona and New Mexico, and throughout much of Mexico including Chihuahua (Allen and Murvosh 1987b). In the USA it has been taken only from the Gila River drainage system.

**Thraulodes gonzalesi*
Traver and Edmunds, 1967

DESCRIPTION.—Adult: Traver and Edmunds (1967). Larva: Traver and Edmunds (1967).

NEW RECORDS.—BYU: Grant Co, Sapillo Cr, jct with Gila R, 1555 m, 26-V-1985, B. Jensen (larva). NMHU: Grant Co, E fork Gila R, nr Grapevine, 1950 m, 12-X-1993, P. Stewart (larvae). PERC: Grant Co, Sapillo Cr, Rd 15, Gila National Forest, 7-V-1981, W.P. McCafferty, A.V. Provonsha, and D. Bloodgood (larvae).

REMARKS.—*Thraulodes salinus* Kilgore and Allen was recently shown by Lugo-Ortiz and McCafferty (1995a) to be a junior synonym of *T. gonzalesi*. Therefore, in addition to the new New Mexico distribution, the species is known from Arizona (Kilgore and Allen 1973), Mexico (including Chihuahua; Allen and Brusca 1978), and Texas (Traver and Edmunds 1967). In New Mexico it has been taken only in the Gila River drainage system.

Thraulodes speciosus
Traver, 1934

DESCRIPTIONS.—Adult: Traver (1934). Larva: Mayo (1969).

PREVIOUS RECORDS.—Durfee and Kondratieff (1995) as *T. arizonicus*: Catron Co (Taylor Cr).

NEW COUNTY RECORDS.—BYU: Grant Co (Turkey Cr).

REMARKS.—*Thraulodes arizonicus* Kilgore and Allen was recently shown to be a junior synonym of *T. speciosus* by Lugo-Ortiz and McCafferty (1995a). This species previously has been known only from Arizona (Traver 1934) and northern Mexico (Allen and Murvosh 1987b, Lugo-Ortiz and McCafferty 1996a), including Chihuahua. Allen and Brusca (1978) may have seen material from New Mexico because they plotted the species in New Mexico on a range map but presented no substantiating data for it. In addition to the new county record cited above, we have seen this species in Catron County from the west fork of the Gila River and White Water Creek. In New Mexico the species is known only from the Gila River drainage system.

Traverella albertana
(McDunnough), 1931

Descriptions.—Adult: McDunnough (1931a) as *Thraulus albertanus* McDunnough; see also Traver and Edmunds (1967). Larva: Edmunds (1948).

PREVIOUS RECORDS.—Kilgore and Allen (1973) as *Traverella castanea*: Catron Co (San Francisco R); Grant Co (Gila R).

NEW COUNTY RECORDS.—NMHU: Santa Fe Co (Rio Grande).

REMARKS.—*Traverella castanea* Kilgore and Allen was shown to be a junior synonym of *T. albertana* by Lugo-Ortiz and McCafferty (1995a). This western species, therefore, is known from Alberta and Saskatchewan south to Chihuahua (see Allen 1973, Allen and Murvosh 1987b, Lugo-Ortiz and McCafferty 1995a, 1996a). Although it is known from the surrounding areas of Arizona, Chihuahua, and Colorado, it is not known from Texas. In New Mexico it has been taken only in the Gila River, upper Rio Grande, and San Francisco River drainage systems.

Oligoneuriidae

Homoeoneuria alleni
Pescador and Peters, 1980

DESCRIPTIONS.—Adult: unknown. Larva: Pescador and Peters (1980).

PREVIOUS RECORDS.—Pescador and Peters (1980): Dona Ana Co (Rio Grande).

REMARKS.—This species was originally described from New Mexico by Pescador and Peters (1980), and those authors also reported it from Chihuahua and Utah. It has since been found in Colorado by Durfee and Kondratieff (1994). In New Mexico it is known only from the lower Rio Grande.

Lachlania dencyannae
Koss, 1970

DESCRIPTIONS.—Adult: Koss and Edmunds (1970) as *L. dencyanna*. Larva: Koss and Edmunds (1970) as *L. dencyanna*.

PREVIOUS RECORDS.—Koss and Edmunds (1970): Grant Co (Gila R).

REMARKS.—This is the only species of North American mayflies known exclusively from

New Mexico and therefore endemic to the state and the Gila River drainage system. It may eventually be found in the Gila River drainage system area of eastern Arizona. We consider this species rare and endangered (see Species of Special Concern below). The ending of the specific epithet of this species has been emended to conform to rules of nomenclature because it was based on a modern female name (Dency Anne) latinized by the original author and thus should have further been given the appropriate genitive ending.

**Lachlania saskatchewanensis*
Ide, 1941

DESCRIPTIONS.—Adult: Ide (1941); see also Edmunds (1951) as *L. powelli* Edmunds. Larva: Edmunds (1951) as *L. powelli.*

NEW RECORDS.—PERC: San Juan Co, San Juan R, Blanco, State Hwy 17 bridge, 10-VIII-1961, D.W. Argyle (larva); San Juan Co, Animas R, Hwy 17 bridge, Farmington, 25-X-1961, D.W. Argyle (larva).

REMARKS.—McCafferty (1996) recently showed *S. powelli* Edmunds from Utah (Edmunds 1951) and Mexico (Lugo-Ortiz and McCafferty 1994) to be a junior synonym of *L. saskatchewanensis.* Thus, *L. saskatchewanensis* occurs from Saskatchewan to Guerrero in Mexico. It is known from the adjacent state of Colorado (McCafferty et al. 1993) but is not reported from Arizona, Chihuahua, or Texas. In New Mexico it has been taken only in the San Juan River drainage system.

Siphlonuridae

Siphlonurus occidentalis (Eaton), 1885

DESCRIPTION.—Adult: Eaton (1885) as *Siphlurus occidentalis* Eaton. Larva: Clemens (1915).

PREVIOUS RECORD.—Traver (1935): Santa Fe Co (Santa Fe R). Peters and Edmunds (1961): San Juan Co (San Juan R). Durfee and Kondratieff (1995): Catron Co (Taylor Cr).

NEW COUNTY RECORDS.—BYU: Grant Co (Gila R, Turkey Cr). NMHU: Otero Co (Agua Chiquita); Taos Co (Rio Hondo). PERC: Grant Co (Buck Cr, Cherry Cr, Little Cr, Sapillo Cr); San Miguel Co (Pecos R); Taos Co (Rio Grande).

REMARKS.—McCafferty et al. (1993) indicated that *S. occidentalis* was the most common species of *Siphlonurus* in western North America. It is known from all USA states adjoining New Mexico except Texas, and was reported from Mexico in adjacent Chihuahua (Lugo-Ortiz and McCafferty 1994) and as far south as Hidalgo (Lugo-Ortiz and McCafferty 1996a). In New Mexico it has been taken in all major drainage systems except the Canadian River drainage system.

FAUNISTICS

Regional Affinities

We have categorized New Mexico mayflies by their general regional geographic affinities and present this data in Table 1. *Western* species are those that have a considerable north–south distribution pattern in western North America. Only those New Mexico mayflies found north of Colorado and Utah and not in Texas (unless restricted to west Texas) are considered in the western species category. Two subcategories of such western mayflies are informative with respect to faunistics. These subcategories segregate those species in which New Mexico is the southern limit of their ranges, and those that occur further south than New Mexico and Arizona. *Southwestern* species are the 2nd main distributional category for New Mexico mayflies. These species occur no further north than Colorado or Utah, and no further east than Oklahoma or Texas. *Widespread* species are the 3rd main distributional category. These are New Mexico species that are western but also occur in at least 1 other large region of the continent, i.e., central, northeastern, or southeastern. *Mexican* species constitute a 4th category. New Mexico species placed in this category are distributed mainly through Mexico and occur no further north than Arizona, New Mexico, or Texas. *Southern* species constitute a 5th category. New Mexico species placed in this category are distributed in the southern USA further east than Texas, and range no further north than New Mexico in the West. *Eastern* species constitute a 6th category. These species occur in the central and northeastern USA in addition to New Mexico.

Table 1 shows that the largest component of the New Mexico mayfly fauna is made up of species generally well represented in the West. Most of these western species are restricted to the USA and Canada, with New Mexico, or New Mexico and Arizona, representing their southern range limit. Moreover, many of these latter species (e.g., *Drunella grandis*, *Epeorus*

TABLE 1. Major geographic affinities of the New Mexico mayfly species. See text for detailed definitions of the distributional categories.

Western species		
Southern limits at NM		Southern limits south of NM
Ameletus sparsatus	†*Ephemerella infrequens*	*Acentrella insignificans*
‡*Ametropus albrighti*	*Heptagenia elegantula*	*Baetis magnus*
†*Attenella margarita*	*Heptagenia solitaria*	*Caenis bajaensis*
†*Baetis bicaudatus*	*Leucrocuta petersi*	*Callibaetis pictus*
†*Cinygmula par*	*Nixe criddlei*	*Camelobaetidius warreni*
†*Drunella coloradensis*	*Nixe simplicioides*	*Lachlania saskatchewanensis*
†*Drunella doddsi*	†*Paraleptophlebia heteronea*	*Paraleptophlebia memorialis*
†*Drunella grandis*	*Procloeon conturbatum*	*Rhithrogena morrisoni*
†*Epeorus albertae*	†*Rhithrogena robusta*	*Serratella micheneri*
†*Epeorus deceptivus*	†*Serratella tibialis*	*Siphlonurus occidentalis*
†*Epeorus longimanus*	†*Timpanoga hecuba*	*Traverella albertana*
Ephemerella inermis		
Southwestern species		
Ameletus doddsianus	*Epeorus margarita*	*Neochoroterpes oklahoma*
Ameletus falsus	*Ephemerella altana*	*Rhithrogena hageni*
Baetis adonis	*Ephemerella mollitia*	*Rhithrogena plana*
Baetis caelestis	*Homoeoneuria alleni*	‡*Rhithrogena vitta*
Baetis notos	*Isonychia intermedia*	*Thraulodes gonzalesi*
Baetodes edmundsi	‡*Labiobaetis apache*	*Tricorythodes condylus*
Camelobaetidius musseri	‡*Lachlania dencyannae*	*Tricorythodes corpulentus*
Choroterpes inornata	*Neochoroterpes kossi*	*Tricorythodes dimorphus*
†*Cloeodes macrolamellus*	*Neochoroterpes nanita*	*Tricorythodes explicatus*
Widespread species		
Acentrella turbida	*Callibaetis fluctuans*	*Isonychia sicca*
Baetis flavistriga	*Ephemera simulans*	*Paraleptophlebia debilis*
Baetis tricaudatus	*Fallceon quilleri*	*Rhithrogena undulata*
Caenis latipennis	*Hexagenia limbata*	*Tricorythodes minutus*
Callibaetis ferrugineus		
Mexican species		
Baetodes deficiens	*Thraulodes brunneus*	*Thraulodes speciosus*
Callibaetis montanus		
Southern species		
Leptophlebia bradleyi		
Eastern species		
Labiobaetis propinquus		

†Species restricted to mountain streams.

‡Found only in the greater Colorado River drainage system.

longimanus) are restricted to mountain streams, and some have their southern range limit in the Rocky Mountain Province of northern New Mexico (e.g., *Serratella tibialis*). None of the western species whose ranges extend into Mexico are restricted exclusively to mountain streams.

The more geographically restricted, southwestern species in New Mexico make up almost as large a component as the western species in New Mexico. None of these species are restricted to mountain streams except *Cloeodes macrolamellus*, but that species is not found at high altitudes. The southwestern species *Labiobaetis apache* and *Lachlania dencyannae* are restricted to the greater Colorado River drainage system.

Thirteen species in New Mexico are considered widespread. Some of these are relatively ubiquitous (e.g., *Baetis tricaudatus*, *Callibaetis ferrugineus*, *Tricorythodes minutus*). *Ephemera simulans* has its southwestern range limit represented in New Mexico. On the other hand, *Caenis latipennis* and *Fallceon quilleri* are widely distributed in much of the USA but also occur through Mexico and Central America. *Acentrella turbida* is widespread but generally found in cool, well-oxygenated water and thus, in New Mexico, is found in mountain streams.

Four species represent an essentially Mexican fauna in New Mexico. Of these, all but *Callibaetis montanus* are restricted in distribution in New Mexico to the Gila River drainage system. Although *C. montanus* has invaded other drainage systems in the state besides the Gila, it is restricted to lower lying areas (San Juan River and southernmost area of the Rio Grande drainage system). *Baetodes deficiens* is notable because its presence in Sapillo Creek (Gila River drainage system) is its only known occurrence in the USA.

Two species show atypical distribution patterns by their presence in New Mexico. *Leptophlebia bradleyi* is a southern species that reaches its westernmost limits in extreme southeastern New Mexico. *Labiobaetis propinquus* is a mainly central USA species that has its southwestern range limit in northeastern and south central New Mexico. We regard its distribution in New Mexico as anomalous since it does not fit any predictable pattern. However, the species may prove to be more widespread in North America than now thought and therefore fall into the widespread category.

We have documented the occurrence of a total of 12 families, 37 genera, and 81 species of mayflies in the state of New Mexico. By comparison with broadly adjoining states, 9 families, 28 genera, and 66 species have been recorded for Arizona (see Lugo-Ortiz and McCafferty 1995a, Zloty 1996); 5 families, 14 genera, and 27 species have been recorded for Chihuahua (see Lugo-Ortiz and McCafferty 1995d, 1996a, McCafferty and Lugo-Ortiz 1996); 14 families, 44 genera, and 100 species for Colorado (see McCafferty et al. 1993, Durfee and Kondratieff 1994); and 11 families, 34 genera, and 92 species for Texas (see Lugo-Ortiz and McCafferty 1995b). The low number of taxa for the Mexican state of Chihuahua is due to the more restricted availability of freshwater habitats in that primarily desert area and also the fact that collecting efforts there have not been on a par with those in the other states mentioned. On the other hand, the relatively high mayfly taxa number in Colorado is due to the diverse topography and array of freshwater habitats available in that state as well as the fact that Colorado has been one of the better worked North American regions with respect to sampling of aquatic macroinvertebrates.

A more informative comparison of the New Mexico mayfly fauna with that of other regions can be made with a comparative index that takes into account the degree of similarity and difference in the faunas of any 2 regions. We have used Sorensen's coefficient of similarity (SC) to compare New Mexico more thoroughly with each of its broadly adjoining states [$SC = 2a/(2a + b + c)$, where a = number of species in common between New Mexico and a comparative state, b = the number of species in New Mexico, and c = the number of species in the comparative state]. The results of such calculations, taking into consideration any recent taxonomic revisions such as Zloty (1996), are as follows: for New Mexico and Arizona, there are 52 species in common and $SC = 0.41$; for New Mexico and Chihuahua, 18 species in common and $SC = 0.35$; for New Mexico and Colorado, 48 species in common and $SC = 0.35$; and for New Mexico and Texas, 22 species in common and $SC = 0.20$.

To a large extent, Arizona mirrors the aquatic environment of New Mexico. The shared mayfly fauna of the 2 states is mainly southwestern but also contains many of the western mountain species (Table 1). This accounts for the high coefficient of similarity for these 2 states. Eighteen of the 27 species thus far known from Chihuahua occur in New Mexico, and this is the main reason for considerable similarity between these states. With respect to relationships with Colorado, just as with Arizona, over half of the New Mexico species are found in Colorado also. However, less than half of the Colorado species are found in New Mexico; this is because of a considerable number of more boreal transcontinental species that occur in Colorado (McCafferty et al. 1993) but not New Mexico. The large number of shared mountain species (all those mountain-restricted species shown under the Western [southern limits New Mexico] categories of Table 1) is offset by the fact that many of the southwestern species in New Mexico do not reach Colorado, thus giving a basically intermediate coefficient of similarity between the 2 states. The low coefficient of similarity between New Mexico and Texas is explained by the fact that only one of the basically eastern and southeastern species of east and central Texas (see Lugo-Ortiz and McCafferty 1995b) reaches New Mexico, and in the same respect, western mountain species of New Mexico do not reach Texas. The vast majority of the 22 species shared by New Mexico and Texas are southwestern or

Mexican species, but some are widespread. *Acentrella insignificans* represents a rare case of a species distributed mainly in the Northwest, but which has also penetrated west Texas, evidently via the Canadian and Pecos River drainage systems.

Drainage System Relationships

In Table 2 we have sorted the New Mexico mayfly species by major drainage system. Species richness is greatest in the Gila system (49 species), followed closely by the Rio Grande (46 species), then Pecos (39 species), Canadian (29 species), and finally San Juan (25 species). The Gila, although not large compared with some other drainages, does have a unique complex of both western mountain species and species that could be considered lowland species, many of which are southwestern or Mexican. The species richness of the Rio Grande and Pecos systems is in large part due to the western mountain species present in headwaters and mountain tributaries, and the range of habitats represented over their relatively long courses, including large, low-lying rivers. The Canadian and San Juan systems are somewhat restricted both in area and in habitats, both primarily with low-lying courses with considerable silting, particularly the San Juan. A number of species collected from the San Juan River prior to 1961 may no longer be present there (see Species of Special Concern below).

If intrastate comparisons of the drainage-system mayfly faunas are made by calculating Sorensen's coefficients (see formulation above), it becomes apparent that the greatest similarity of any 2 systems is that shown by the Gila and Rio Grande systems (Fig. 2), which also happen to be the richest systems. The Pecos system is also relatively similar to both the Gila and Rio Grande (Fig. 2). The least similarity is shown between the Gila and Canadian systems, probably due to the distance between them, compounded by the fact that one is a western drainage and the other an eastern drainage, and by their overall dissimilarity in habitat availability. The Canadian system has only 14 species in common with the San Juan system and another 14 in common with the Gila system. Factoring in the faunal size of the systems in question, however, shows that the Canadian and San Juan systems have a greater similarity than the Canadian and Gila systems (Fig. 2). By summing all intra-drainage coefficients for each of the drainage systems, we can see that the Rio Grande system fauna is most representative of the entire New Mexico fauna, whereas the San Juan and Canadian system faunas are least representative of the state.

Eighteen New Mexico mayfly species are known exclusively from western drainages in the state (San Juan, Zuni, San Francisco, Gila), and 23 species are known exclusively from eastern drainages (essentially all drainages east of the continental divide: Dry Cimarron, Canadian, Rio Grande, Pecos; see Table 2, Fig. 1). The genera to which these exclusive drainage system species belong can be considered with respect to their recent biogeographic origins (Edmunds et al. 1976, McCafferty et al. 1992). Twelve of the 18 species confined to the western drainage systems are species that are members of genera that have recent Neotropical biogeographic origins (*Baetodes*, *Camelobaetidius*, *Leptohyphes*, *Tricorythodes*, *Thraulodes*, *Lachlania*). On the other hand, nearly all species (22 of 23) that are found exclusively in eastern drainages in New Mexico belong to genera that have boreal Nearctic biogeographic origins (*Ameletus*, *Baetis*, *Labiobaetis*, *Caenis*, *Attenella*, *Drunella*, *Ephemerella*, *Serratella*, *Timpanoga*, *Ephemera*, *Hexagenia*, *Cinygmula*, *Epeorus*, *Rhithrogena*, *Isonychia*, *Neochoroterpes*, *Leptophlebia*, *Paraleptophlebia*, *Homoeoneuria*). This comparison suggests that the greater Colorado drainage system has been a major northern dispersal corridor for mayflies during its 3.5-million-year existence. It also suggests that the greater Rio Grande drainage system has not been amenable to northern dispersal of austral taxa, but has been primarily colonized from the north. However, mountain species found exclusively in the eastern drainage systems (there are 9 of these) evidently have been limited to the northern part of the state by topography. The 38 species of New Mexico mayflies that occur in both eastern and western drainage systems in the state belong to a mix of Nearctic and Neotropical genera and demonstrate that none of the drainage systems in New Mexico should be considered one-way corridors.

Species of Special Concern

Recent studies of the mayflies of the Southwest indicate that only 1 endemic species occurs in New Mexico. It is *Lachlania dencyannae*, a

TABLE 2. Drainage system distributions of New Mexico mayfly species.

San Juan (including Zuni)

Acentrella insignificans
Ametropus albrighti
Baetis flavistriga
Baetis tricaudatus
Callibaetis ferrugineus
Callibaetis montanus
Callibaetis pictus
Camelobaetidius warreni
Ephemerella inermis
Ephemerella mollitia
Heptagenia elegantula
Heptagenia solitaria
Labiobaetis apache
Lachlania saskatchewanensis
Leptohyphes apache
Nixe criddlei
Nixe simplicioides
Paraleptophlebia memorialis
Procloeon conturbatum
Rhithrogena morrisoni
Rhithrogena undulata
Serratella micheneri
Siphlonurus occidentalis
Tricorythodes explicatus
Tricorythodes minutus

Gila (including San Francisco)

Acentrella insignificans
Ameletus doddsianus
Baetis bicaudatus
Baetis caelestis
Baetis magnus
Baetis notos
Baetis tricaudatus
Baetodes deficiens
Baetodes edmundsi
Caenis bajaensis
Callibaetis ferrugineus
Callibaetis montanus
Callibaetis pictus
Camelobaetidius musseri
Camelobaetidius warreni
Choroterpes inornata
Cloeodes macrolamellus
Drunella doddsi
Epeorus deceptivus
Epeorus longimanus
Epeorus margarita
Drunella grandis
Ephemerella altana
Ephemerella inermis
Fallceon quilleri
Heptagenia solitaria
Isonychia intermedia
Lachlania dencyannae
Leptohyphes apache
Leucrocuta petersi
Neochoroterpes kossi
Nixe criddlei
Nixe simplicioides
Paraleptophlebia debilis
Paraleptophlebia memorialis
Rhithrogena plana
Rhithrogena robusta
Rhithrogena undulata
Rhithrogena vitta
Serratella micheneri
Siphlonurus occidentalis
Thraulodes brunneus
Thraulodes gonzalesi
Thraulodes speciosus
Traverella albertana
Tricorythodes condylus
Tricorythodes corpulentus
Tricorythodes dimorphus
Tricorythodes minutus

Canadian (including Dry Cimarron)

Acentrella insignificans
Baetis bicaudatus
Baetis magnus
Baetis notos
Baetis tricaudatus
Baetodes edmundsi
Caenis bajaensis
Camelobaetidius warreni
Choroterpes inornata
Drunella doddsi
Drunella grandis
Ephemerella altana
Ephemerella inermis
Heptagenia elegantula
Heptagenia solitaria
Labiobaetis propinquus
Leucrocuta petersi
Neochoroterpes nanita
Neochoroterpes oklahoma
Nixe criddlei
Nixe simplicioides
Paraleptophlebia debilis
Paraleptophlebia heteronea
Paraleptophlebia memorialis
Rhithrogena morrisoni
Rhithrogena undulata
Serratella micheneri
Tricorythodes explicatus
Tricorythodes minutus

notably distinct and unique mayfly with a restrictive habitat (Koss and Edmunds 1970). Most other species once thought to be endemic to New Mexico have eventually been found in Arizona, often in the same drainage system (middle or lower Colorado River drainage system). *Lachlania dencyannae* deserves special attention for other reasons, beside its being endemic. It is limited in distribution to the Gila River drainage system. *Camelobaetidius musseri, Cloeodes macrolamellus, Rhithrogena vitta, Tricorythodes condylus, T. corpulentus, Neochoroterpes kossi, Thraulodes brunneus, T. gonzalesi,* and *T. speciosus* are additional New Mexico species that are found only in the Gila River drainage system. This drainage system can therefore be viewed as a refugium in New Mexico for certain southwestern species. In addition, *Lachlania* is a highly unusual group of mayflies with rapid flight habits and associated wing morphology unique among the Ephemeroptera (see Edmunds et al. 1976) and a molting process unique among all insects (see Edmunds and McCafferty 1988). Given the highly restricted range and remarkable nature of this mayfly species, we recommend that *L. dencyannae* be given special consideration as a rare and endangered species, both at the state and federal levels. Because of the degradation of the Gila River, especially in Arizona (see e.g., McNamee 1994), and impending degradation in New Mexico, we suggest

TABLE 2. Continued.

Rio Grande

Acentrella insignificans
Acentrella turbida
Ameletus doddsianus
Ameletus falsus
Attenella margarita
Baetis bicaudatus
Baetis magnus
Baetis tricaudatus
Callibaetis ferrugineus
Callibaetis montanus
Callibaetis pictus
Choroterpes inornata
Drunella coloradensis
Drunella doddsi
Drunella grandis
Epeorus albertae
Epeorus deceptivus
Epeorus longimanus
Epeorus margarita
Ephemera simulans
Ephemerella altana
Ephemerella inermis
Ephemerella infrequens
Fallceon quilleri
Heptagenia solitaria
Homoeoneuria alleni
Isonychia intermedia
Isonychia sicca
Nixe criddlei
Nixe simplicioides
Paraleptophlebia debilis
Paraleptophlebia heteronea
Paraleptophlebia memorialis
Rhithrogena hageni
Rhithrogena morrisoni
Rhithrogena plana
Rhithrogena robusta
Rhithrogena undulata
Serratella micheneri
Serratella tibialis
Siphlonurus occidentalis
Timpanoga hecuba
Traverella albertana
Tricorythodes dimorphus
Tricorythodes explicatus
Tricorythodes minutus

Pecos

Acentrella insignificans
Acentrella turbida
Ameletus falsus
Ameletus sparsatus
Attenella margarita
Baetis adonis
Baetis bicaudatus
Baetis caelestis
Baetis magnus
Baetis tricaudatus
Caenis latipennis
Callibaetis ferrugineus
Callibaetis fluctuans
Callibaetis pictus
Choroterpes inornata
Cinygmula par
Drunella coloradensis
Drunella doddsi
Drunella grandis
Epeorus deceptivus
Epeorus longimanus
Ephemerella altana
Ephemerella inermis
Fallceon quilleri
Hexagenia bilineata
Labiobaetis propinquus
Leptophlebia bradleyi
Neochoroterpes oklahoma
Nixe criddlei
Nixe simplicioides
Paraleptophlebia debilis
Paraleptophlebia memorialis
Rhithrogena morrisoni
Rhithrogena undulata
Serratella micheneri
Siphlonurus occidentalis
Timpanoga hecuba
Tricorythodes explicatus
Tricorythodes minutus

that the other Gila River drainage system mayfly species, mentioned above, minimally be considered at risk.

We consider the following mayfly species rare or, in some cases, possibly recently extirpated in New Mexico. *Ametropus albrighti* is a sand-dwelling mayfly with very specific habitat requirements (see Clifford and Barton 1979) that has been taken only in the San Juan River in New Mexico and the Green River system in the region where Colorado, Wyoming, and Utah meet (Allen and Edmunds 1976). Although such sand-dwelling species can be difficult to sample (McCafferty 1991), *A. albrighti* has not been taken in New Mexico since 1935. Sublette et al. (1990) discussed the changes to the San Juan River related to a recent host of large-scale irrigation facilities in the San Juan Basin and construction of the Navajo Dam. *Callibaetis fluctuans* is a common species elsewhere, but in New Mexico it has been taken only from a single sample from Castle Creek in Eddy County (lower Pecos River drainage system). It may have only recently invaded the state, and we expect that it may become more widespread if it is relatively vagile as is typical of other species in the genus (McCafferty et al. 1992). *Procloeon conturbatum* is known in New Mexico only from adult males taken at the San Juan River. *Leptophlebia bradleyi* is known only from a single sample from Eddy County, which apparently is the westernmost record of this southern USA species. *Neochoroterpes nanita* is known from only 1 sample from the Canadian River in San Miguel County. Otherwise, it is known only from central and east central Texas (Henry 1993, Lugo-Ortiz and McCafferty 1995b). *Rhithrogena hageni* is known only from an isolated fringe population in the Red River in Taos County, upper Rio Grande drainage system. Although also rare in Arizona, it is relatively common in Colorado.

Hexagenia bilineata is a large, common, and well-known species in eastern and central areas

	G	C	R	P
S	15[.29]	13[.33]	16[.31]	14[.27]
G		13[.25]	30[.39]	22[.36]
C			17[.31]	15[.31]
R				25[.37]

Fig. 2. Matrix of New Mexico species shared by, and Sorensen's coefficients of similarity [in brackets] between, major drainage systems in New Mexico. S = San Juan + Zuni, G = Gila + San Francisco, C = Canadian + Dry Cimarron, R = Rio Grande, P = Pecos.

of North America. In New Mexico, however, its distribution is disjunct, the population is unusual (see Species Accounts above), and the single habitat where it is found is a one-of-a-kind area in the state. It consists of a 1-km-long, 2-m-deep pool with fine, calcareous sediments. It is located just upstream from Harkey crossing on the Black River (Eddy County). We doubt there is another habitat with this type of burrowing substrate (required by *Hexagenia* mayflies) in New Mexico. The road crossing mentioned above acts as a partial dam across the limestone basin, and any alteration of the crossing or roadwork would seriously affect the depositional nature and sediment trapping feature of the extensive pool.

Homoeoneuria alleni is known somewhat north and south of New Mexico. In New Mexico it has been taken only once from the lower Rio Grande in Dona Ana County. However, we expect that this sand-dwelling species is difficult to collect in larger rivers. Likewise, *Lachlania saskatchewanensis*, known only from the San Juan River drainage system in New Mexico, is also difficult to sample and in reality may not be rare.

Baetis adonis, *Ephemerella mollitia*, and *Leucrocuta petersi* are apparently rare North American species. *Baetis adonis* is known only from the San Gabriel Mountains of southern California and the upper Pecos River in the foothills of the Sangre de Cristo Mountains in San Miguel County, New Mexico. *Ephemerella mollitia* is also known only from California and New Mexico. Although it has not been reported from the San Juan River since 1935 and this singular New Mexico record was questioned by Allen and Edmunds (1965), the fact that the species is also known in California from the San Gabriel Mountains (as is *B. adonis* above) would possibly add credence to the New Mexico report. If it was taken from New Mexico, it may now be extirpated there due to alteration of habitats in the San Juan River that have occurred in the last half of this century. It is possible that *Leucrocuta petersi* presently occurs only in New Mexico. Outside of New Mexico the species has been known only from the Green River of northeastern Utah and southwestern Wyoming. However, the species may now be extirpated in these latter states because the construction of Flaming Gorge Dam has had some detrimental effects on mayflies of that area (Edmunds personal communication), and *L. petersi* has not been found there subsequent to the collections of the type material (1945, 1962; Allen 1966). The species apparently is common in the Gila River drainage system in New Mexico, and it has also been taken in a sample from the Canadian River drainage system in another part of the state.

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HOLOCENE VEGETATION AND HISTORIC GRAZING IMPACTS AT CAPITOL REEF NATIONAL PARK RECONSTRUCTED USING PACKRAT MIDDENS

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ABSTRACT.—Mid- to late-Holocene vegetation change from a remote high-desert site was reconstructed using plant macrofossils and pollen from 9 packrat middens ranging from 0 to 5400 yr in age. Presettlement middens consistently contained abundant macrofossils of plant species palatable to large herbivores that are now absent or reduced, such as winterfat (*Ceratoides lanata*) and ricegrass (*Stipa hymenoides*). Macrofossils and pollen of pinyon pine (*Pinus edulis*), sagebrush (*Artemisia* spp.), and roundleaf buffaloberry (*Shepherdia rotundifolia*) were also recently reduced to their lowest levels for the 5400-yr record. Conversely, species typical of overgrazed range, such as snakeweed (*Gutierrezia sarothrae*), viscid rabbitbrush (*Chrysothamnus visidiflorus*), and Russian thistle (*Salsola* sp.), were not recorded prior to the historic introduction of grazing animals. Pollen of Utah juniper (*Juniperus osteosperma*) also increased during the last 200 yr. These records demonstrate that the most severe vegetation changes of the last 5400 yr occurred during the past 200 yr. The nature and timing of these changes suggest that they were primarily caused by 19th-century open-land sheep and cattle ranching. The reduction of pinyon and sagebrush concurrent with other grazing impacts suggests that effects of cattle grazing at modern stocking levels may be a poor analog for the effects of intense sheep grazing during drought.

Key words: Holocene vegetation history, grazing impacts, packrat middens, fossil pollen, presettlement vegetation.

STUDY AREA

This purpose of this study was to produce a Holocene vegetation history of Capitol Reef National Park, reconstructing past changes in vegetation and relating those changes to their most probable causes. Packrat midden chronologies were developed from several sites (Cole 1992), but only the most complete series from a single site, collected from the Hartnet Draw site, is reported here. Seven fossil and 2 modern middens were collected from Hartnet Draw in northern Capitol Reef National Park (38°15′N, 111°20′W; Fig. 1). This site, at 1920 m elevation in Wayne County, Utah, was chosen because of its remote location, free from most anthropogenic disturbances other than grazing, and the abundant fossil packrat middens.

The site is underlain by the Salt Creek Member of the Morrison Formation, which forms many overhangs protecting the fossil packrat middens (Fig. 2A). Today, the most abundant plant species are Utah juniper (*Juniperus osteosperma*), Bigelow sagebrush (*Artemisia biglovii*), big sagebrush (*A. tridentata*), snakeweed (*Gutierrezia sarothrae*), Torrey ephedra (*Ephedra torreyana*), viscid rabbitbrush (*Chrysothamnus visidiflorus*), and central pricklypear (*Opuntia polyacantha*; Table 1). Low areas with thicker soil support a sparse growth of grasses: ricegrass (*Stipa hymenoides*), sand dropseed (*Sporobolus cryptandrus*), and blue grama (*Bouteloua gracilis*). Plant taxonomy follows Welsh et al. (1987).

Mean annual precipitation at the site is close to the 18 cm yr^{-1} recorded at Fruita, 15 km to the southwest at 1670 m elevation (Heil et al. 1993). Precipitation is bi-seasonal, with winter and late summer peaks. Temperature extremes are great at this arid continental site: a mean January minimum temperature at Fruita of −8°C and a mean July maximum of 33°C.

GRAZING HISTORY.—Historical records mention no disturbances to this area other than the introduction of exotic herbivores during the mid-19th century. Native large herbivores that may have been present in the study area during the last 5000 yr include bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and possibly bison (*Bison bison*) and elk (*Cervus elaphus;* Van Gelder 1928, Mead et al. 1991).

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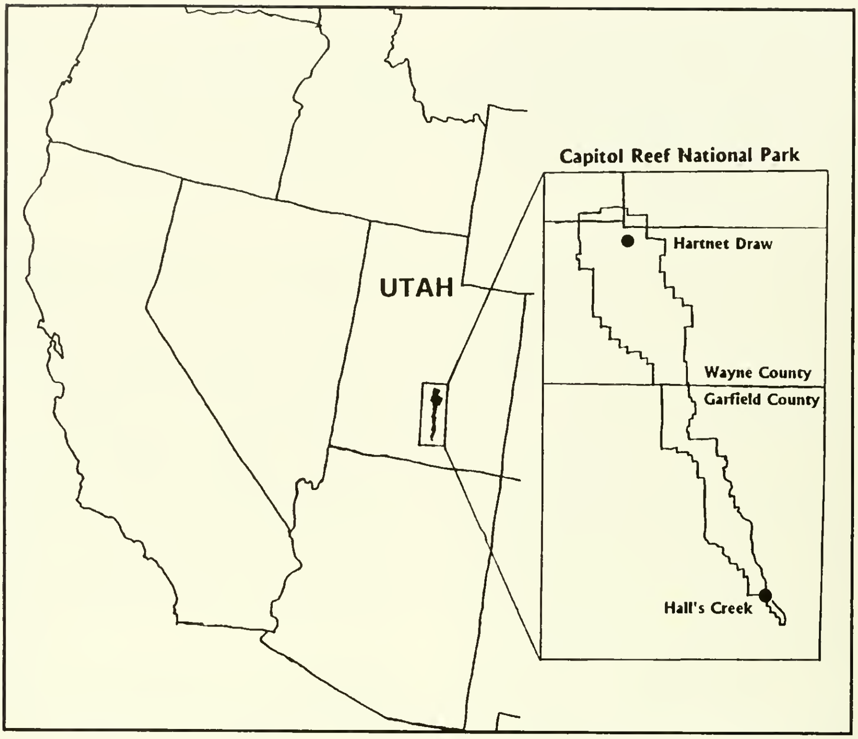

Fig. 1. Map showing site location.

Native North American equids (horses and asses) became extinct before 10,000 yr B.P. (Mead and Meltzer 1984). Eurasian horses and asses (*Equus* spp.) were introduced to New Mexico by Spanish colonists as early as A.D. 1598 (Underhill 1971). By the late 1600s feral horses were reported in parts of the West, but it is not likely that they existed in the study area prior to the 1800s.

In the late 1800s introduced herbivore populations increased dramatically in southern Utah with the widespread increase in open-land grazing. Livestock grazing within and near Capitol Reef National Park has been documented since at least the 1870s (Frye 1995). The earliest detailed herbivore population estimates from the Capitol Reef area are from summer grazing permits issued for Powell (now part of Dixie) National Forest (Frye 1995). In 1909 the Forest Service issued permits for 67,000 sheep and 11,000 cattle. The animals grazing these high summer pastures presumably spent the winter in the lower adjacent areas of Capitol Reef National Park.

A Bureau of Land Management survey described past use at the Hartnet Draw site:

> Prior to the passage of the Taylor Grazing act in 1934, large numbers of livestock were brought from Wayne, Sevier, and Emery Counties to winter on these lands. Many of the animals remained on the range yearlong, resulting in the progressive destruction of soils and vegetation. Reports from stockmen in the area indicate that many trespass horses used the area until about 1955. Prior to 1946 there were at least 163 cattle and 20 horses yearlong in this area (Hartnet Allotment File, 1966).

Currently, the area is grazed under an allotment issued by Capitol Reef National Park.

RECONSTRUCTING PAST VEGETATION.—Fossil packrat middens are valuable sources of paleoecological information in arid regions of the southwestern United States (Betancourt et al. 1990, Cole 1990). Plant fossils in packrat middens, often identifiable to the species level, grew close to the midden, most likely within 50 m. Because plant identification and location can be precisely known, this method has extremely high spatial and taxonomic resolution compared to other methods of reconstructing past vegetation.

Studies comparing trees and shrubs at midden sites with plant specimens from modern middens typically report similarities exceeding

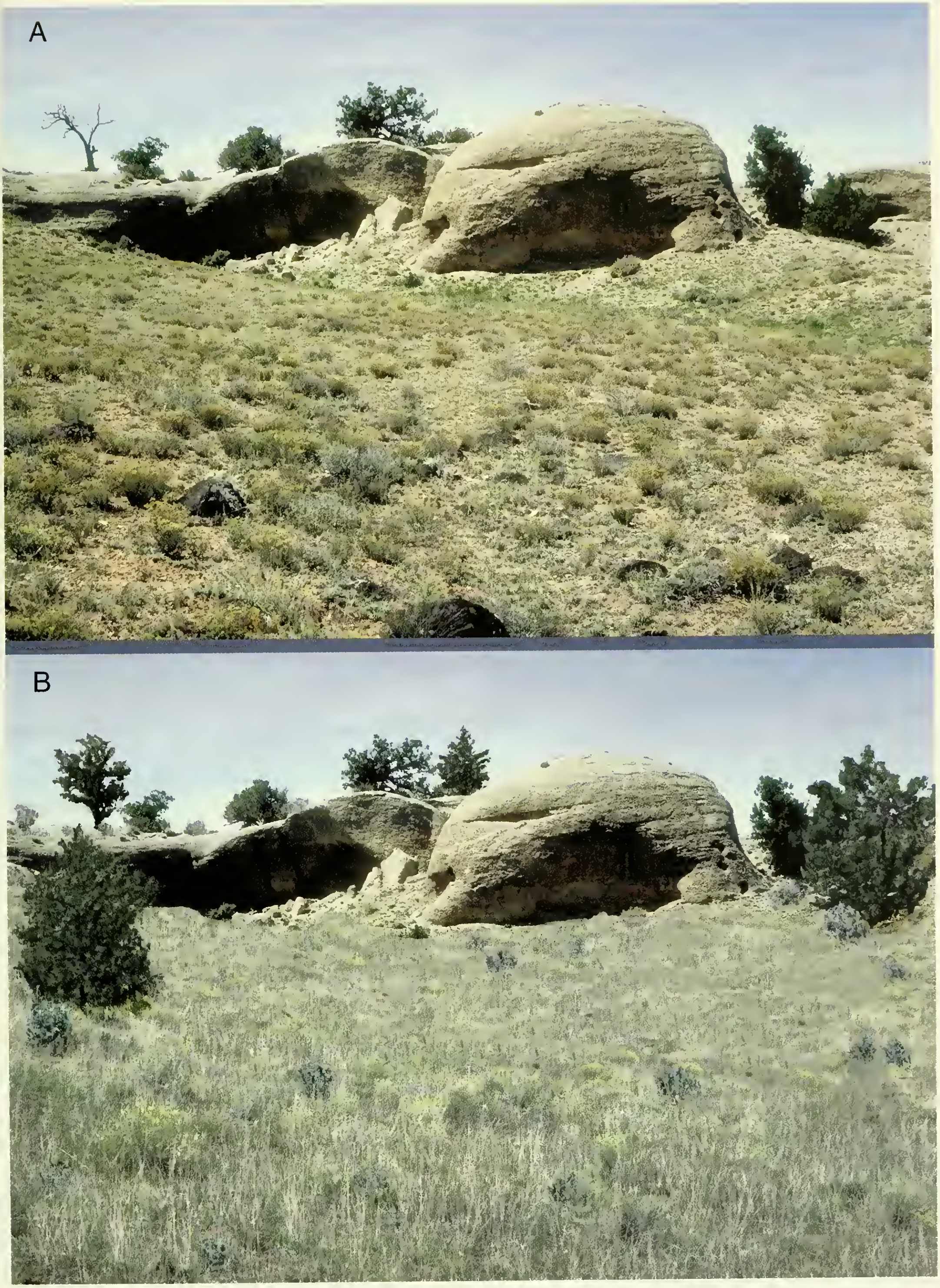

Fig. 2. A, Photograph of Hartnet Draw study site showing shelter where middens #'s 1–4 were collected. B, Reconstructed image of study site with presettlement vegetation as visualized from fossil data.

TABLE 1. Plant macrofossil concentrations from Hartnet Draw middens in $\log_{10}$ concentration/kg of washed matrix. Modern percent cover classes are estimated from a relevé of 30-m radius. Coverage classes: 3 = >3% cover, 2 = 1–3% cover, 1 = <1% cover, R = rare (located outside of relevé).

	Midden #	#3	#2	#8	#1a	#7b	#9	#5	#6
	Midden age (yr B.P.)	0	330	630	1020	1275	2570	3615	5450
	Modern relevé (Cover class)	$\log_{10}$ concentration/kg of washed matrix							
TREES, SHRUBS, AND SUCCULENTS									
Artemisia (sec. tridentatae)	3	0.9	1.8		2.8	2.8	1.8	1.3	2.0
Atriplex spp.	2	2.8	3.3	3.0	4.3	3.1	3.2	2.8	4.1
Brickellia scabra	2	1.3							
Chrysothamnus sp.	2	1.6							
Cowania mexicana	2	2.0	1.9	1.9	2.6	3.1	2.5	2.9	1.2
Ephedra spp.	2	1.7	0.5			3.1	1.3		2.3
Ceratoides lanata			2.0	1.7	3.6	2.4	2.5	2.3	3.0
Gutierrezia sarothrae	3	2.0	1.3						
Heterotheca sp.	1	0.9							1.8
Hymenopappus	1	1.9							
Juniperus osteosperma	3	3.4	3.9	3.8	4.3	4.3	4.3	4.0	4.1
Machaeranthera grindeliodes	1	0.4							
Opuntia polyacantha	2	3.1	3.7	3.1	4.3	4.2	3.5	3.9	3.9
Pediocactus/Echinocereus	1		1.1		1.4		2.1	2.4	2.1
Pinus edulis	R		2.0	2.8	4.7	2.6	4.1	3.0	2.0
Salsola sp.	1	1.3							
Sarcobatus sp.	R	1.0							
Shepherdia rotundifolia	1			2.5		1.8			3.0
Yucca angustissima	R	1.0						1.9	
HERBS AND GRASSES									
cf. *Amaranthus* sp.		2.3				1.7	1.9	1.6	1.6
Astragalus mollissimus	1	0.9							
Aristida purpurea	2								
Bouteloua gracilis	3		1.7		1.4	2.2			
Chryptantha spp.	3	0.8	0.5			1.3			1.2
Descurania pinnata	3								
Eriogonum sp.		1.0				1.8			
Erioneuron pulchellum	1								
Euphorbia sp.	1		1.7						1.7
Hilaria sp.								1.3	
Hymenoxys acaulis	1								
Lappula occidentalis	1	0.4	0.9		0.8	1.8			
Lepidium densiflorum	1	1.8	0.5			1.3			2.3
Peanut shell		0.9							
Phacelia							1.3		
Plantago			0.9			1.4			
Sphaeralcea coccinea	1		1.3		1.2	2.2			2.5
Sporobolis spp.	3		0.9					1.3	
Stipa hymenoides	3		1.5	1.7	1.6	1.3	2.8	1.9	1.7
Stipa sp.							1.3		1.2
Streptanthella longirostris	1								

80% using a Sorensen's index of similarity (Cole 1985, Cole and Webb 1985, Spaulding et al. 1990, Frase and Sera 1993), especially when small macrofossils (<2 mm) are identified using a 10X microscope. Similarity with forbs and grasses has been reported to be lower (Frase and Sera 1993), but inventories of current forbs are usually incomplete due to seasonal and yearly variability in the forb flora, and identification of diverse forbs and grasses within midden assemblages is very challenging.

The quantitative correlation between species abundance and midden specimens is complex (Spaulding et al. 1990). Plant species producing abundant, readily identifiable plant parts (e.g., *Atriplex* leaves), or packrat food items (e.g., juniper), or plants having deterrence values in protecting packrats from predators (e.g., cactus spines), tend to occur in the highest numbers within middens. But perennial species that are abundant near middens are most often represented by high numbers of plant specimens, while less abundant species, or those further from middens, are represented by fewer specimens. As a result, interpreting changes from midden assemblages requires experience with macrofossil types (leaves, twigs, flowers, seeds) and abundances typically found for that species. This element of judgment is present in any retrospective study. For example, fossil pollen magnifies the presence of wind-pollinated plants while insect-pollinated species may not be represented at all. Phytolith studies detect only those species producing identifiable opal phytoliths. Historical writings record only those species of interest to the writers. Repeat photography is useful only for those species identifiable in photographs. Midden records can be viewed as representing something similar to a plant relevé (Mueller-Dombois and Ellenberg 1974) from the past. This relevé contains a detailed species list, but also more complex information on past species abundance comparable to coverage classes.

Fossil pollen within middens can also be analyzed (King and Van Devender 1977, Thompson 1985, Davis and Anderson 1988), emphasizing different types of vegetation and representing a larger source area than the plant macrofossils. Interpretation of fossil pollen abundances, like macrofossil abundances, requires caution and experience, as some species are better represented than others. By considering both macrofossil and pollen records, we can achieve a more comprehensive understanding of past environments.

MATERIALS AND METHODS

We collected 7 of the 8 middens within a radius of about 200 m from a small shelter (Fig. 2). The 8th was found 1 km east of the shelter. Using a hammer and chisel, we separated approximately 1 kg of each midden from larger masses and returned the samples to the laboratory. Samples were then dissected, producing horizontally stratified subsamples typically measuring about 15 × 20 cm and several centimeters thick. Weathering rinds and large rocks were removed from each subsample, yielding 300–600 g of hardened midden material. This sample was then weighed and disaggregated in water. Two unconsolidated middens (Hartnet Draw #'s 3 and 4) were considered modern because of the presence of green leafy material, cow feces, and a peanut shell.

Pollen samples were taken from the wash water after several days of soaking, and the pollen was separated using standard methods (Faegri and Iversen 1975). Macrofossils of 1 modern midden, Hartnet Draw #4, could not be analyzed because the midden had been burned, charring much of the plant debris. The pollen content of this midden, however, was not destroyed by the fire. Packrat debris piles are often burned in rangeland shelters, most likely to eliminate the rats that occupy a pleasant shelter.

After sieving vegetable debris, fecal pellets, and rocks from the dissolved middens with a 1-mm sieve, we mixed, dried, and weighed the resulting matrix, producing 100–200 g of washed midden matrix. The dried matrix was sorted by hand under a 10X dissecting microscope. Packrat fecal pellets and rocks were removed and weighed. Identifiable plant macrofossils, vertebrate bones, and insect fossils were identified, counted, labeled, and stored in plastic vials.

Six to 13 g of packrat fecal pellets were submitted to radiocarbon laboratories for dating. Hartnet Draw #5 was dated at 3615 ± 70 yr B.P. using a single *Pinus* needle after the initial pellet sample yielded an impossible result of 142% modern carbon. Some type of sample contamination with artificial carbon isotopes or sample mislabeling is suspected, as it is impossible to contaminate an old sample with enough modern natural carbon isotopes to yield such a high number. Calendar year ranges for radiocarbon ages were calculated using Stuiver and Reimer's (1993) calibration program.

Data on midden contents were quantified by number, weight, percent of identified specimens, and $\log_{10}$ of macrofossil concentration in midden matrix. To compensate for variability between middens, we adjusted midden matrix weights by subtracting the weight of rocks and pellets from the dried washed matrix weight before calculating the concentration as suggested in Betancourt (1990). Using $\log_{10}$ of macrofossil concentration calculates a number similar to the semi-quantitative abundance scale used by several other authors, but it has the advantage of being quantitative.

TABLE 2. Ages of middens based on radiocarbon dates. Radiocarbon ages are calibrated to calendar years based on Stuiver and Reimer (1993). %MC = percent modern carbon (sample postdates atmospheric testing of nuclear weapons).

Sample name	Radiocarbon date	δ ^{13}C	Lab ID No.	Calendar year range (at one sigma)	Material dated
Hartnet Draw #4	Modern debris pile (not dated)				
Hartnet Draw #3	137 ± 1.2 %MC	–22.2	A-5197	AD 1960–1986	*Neotoma* pellets
Hartnet Draw #2	330 ± 60	–21.8	A-5204	AD 1495–1643	*Neotoma* pellets
Hartnet Draw #8	630 ± 100	–21.2	GX-16259	AD 1280–1410	*Neotoma* pellets
Hartnet Draw #1a	1020 ± 70	–21.7	A-5203	AD 898–1152	*Neotoma* pellets
Hartnet Draw #7b	1275 ±110	–20.8	GX-15554	AD 640–890	*Neotoma* pellets
Hartnet Draw #9	2570 ±135	–21.8	GX-15553	889–434 BC	*Neotoma* pellets
Hartnet Draw #5	3615 ± 70		AA-6447	2128–1889 BC	*Pinus edulis* needle
Hartnet Draw #6	5450 ± 90	–21.8	A-5205	4363–4235 BC	*Neotoma* pellets

We used the program CONISS (Grimm 1987) on the plant macrofossil and pollen results to conduct a stratigraphically constrained cluster analysis using a square root transformation and Edwards and Cavalli-Sforza's chord distance as a dissimilarity coefficient. The square root transformation makes the skewed distributions of abundant species more closely conform to normal distributions. Plant taxa occurring in only a single midden sample were deleted from the analysis to eliminate false positive correlations due to shared absences. These deletions cause any differences between the modern and fossil middens to be understated.

RESULTS

MIDDEN AGE.—The 9 middens ranged in age from modern to 5450 yr B.P. (Table 2). Hartnet Draw #3 contained 137% modern carbon ("modern" is defined as A.D. 1950) and thus postdates atmospheric testing of nuclear weapons. Seven middens dated to presettlement times.

PLANT MACROFOSSILS.—All of the middens contain abundant macrofossils of Utah juniper (*Juniperus osteosperma*), saltbush (*Atriplex* spp.), cliff rose (*Cowania mexicana*), and prickly pear (*Opuntia* sp.), which are all plentiful at the site today (Table 1, Fig. 3). The presettlement middens also contain pinyon pine (*Pinus edulis*), winterfat (*Ceratoides lanata*), sagebrush (*Artemisia* sp.), and ricegrass (*Stipa hymenoides*), which are rare or absent from the single modern midden analyzed for macrofossils (Hartnet #3). Winterfat was not observed during the fieldwork, and pinyon pine was rare in the area. The rarity or absence of sagebrush and ricegrass from the modern midden suggests that they are less common now than prior to settlement. Similarly, globe mallow (*Sphaeralcea* sp.), needlegrass (*Stipa* sp.), blue grama (*Bouteloua gracilis*), dropseed (*Sporabolis cryptandrus*), and roundleaf buffaloberry (*Shepherdia rotundifolia*) are common in presettlement middens but absent from the 1 modern midden.

In contrast, Hartnet #3, the modern midden, is the only midden containing viscid rabbitbrush (*Chrysothamnus visidiflorus*), greasewood (*Sarcobatus vermiculatus*), and Russian thistle (*Salsola* sp.) macrofossils. Only the 2 most recent middens (#3 and #2) contain snakeweed (*Gutierrezia sarothrae*). Rabbitbrush, snakeweed, and Russian thistle are frequent at the site today. The absence of these species from presettlement middens indicates that these species were formerly absent, or so infrequent as to not be represented.

The cluster analysis (right side, Fig. 3) demonstrates the difference between the modern macrofossil assemblage and other assemblages. It is the primary branch in the dendrogram even though the single occurrences of rabbitbrush, greasewood, and Russian thistle in the modern midden were disregarded in the analysis.

POLLEN SAMPLES.—Results of the pollen analysis (Fig. 4) are similar to those from plant macrofossils. Presettlement middens contained much more pine and sagebrush pollen than the 2 modern samples (#3 and #4). Similarly, percentages of grass and buffaloberry pollen were generally higher in presettlement middens. In contrast, only the 2 modern middens contained pollen of the exotic Russian thistle and high amounts of juniper pollen. Like the macrofossil cluster analysis, the pollen cluster analysis (right side of Fig. 4) showed that modern samples are very different from all presettlement middens.

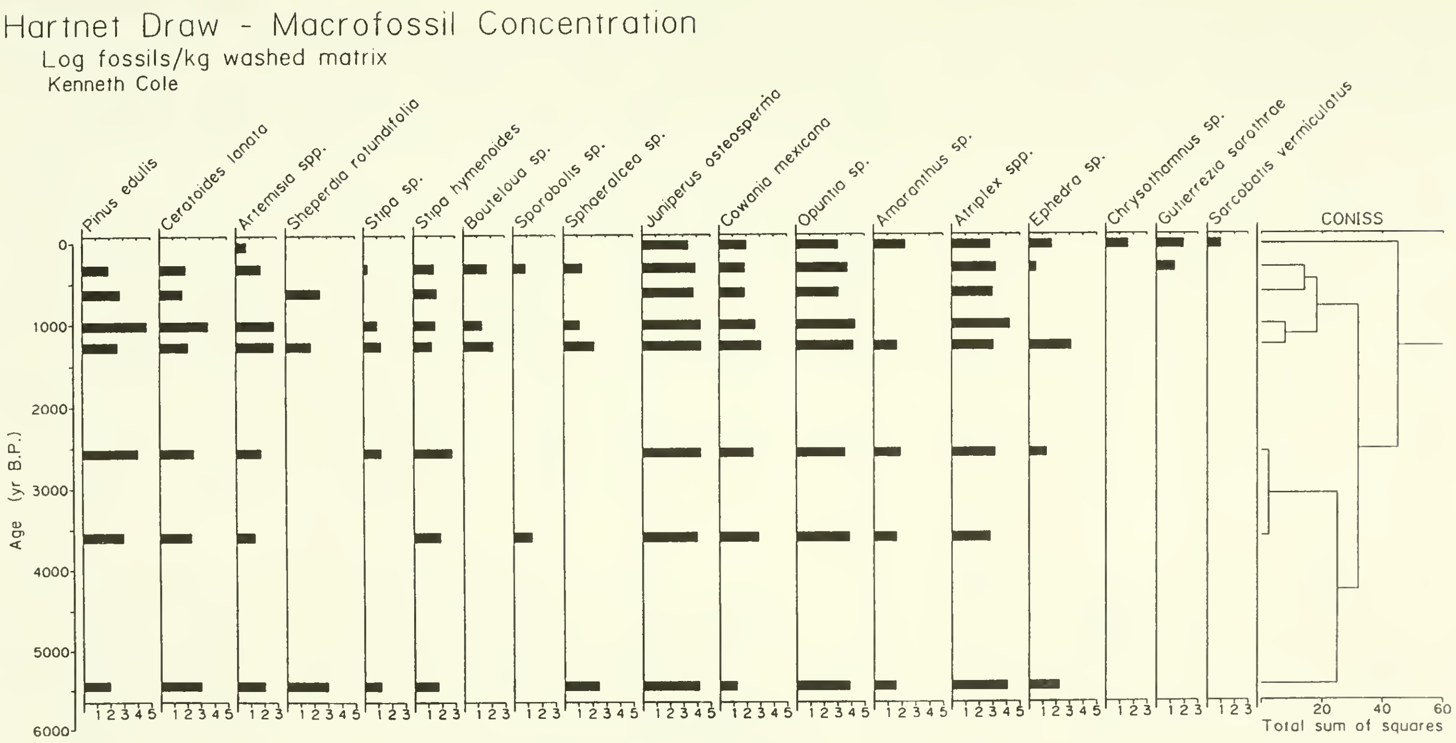

Fig. 3. Plant macrofossils from Hartnet Draw packrat middens.

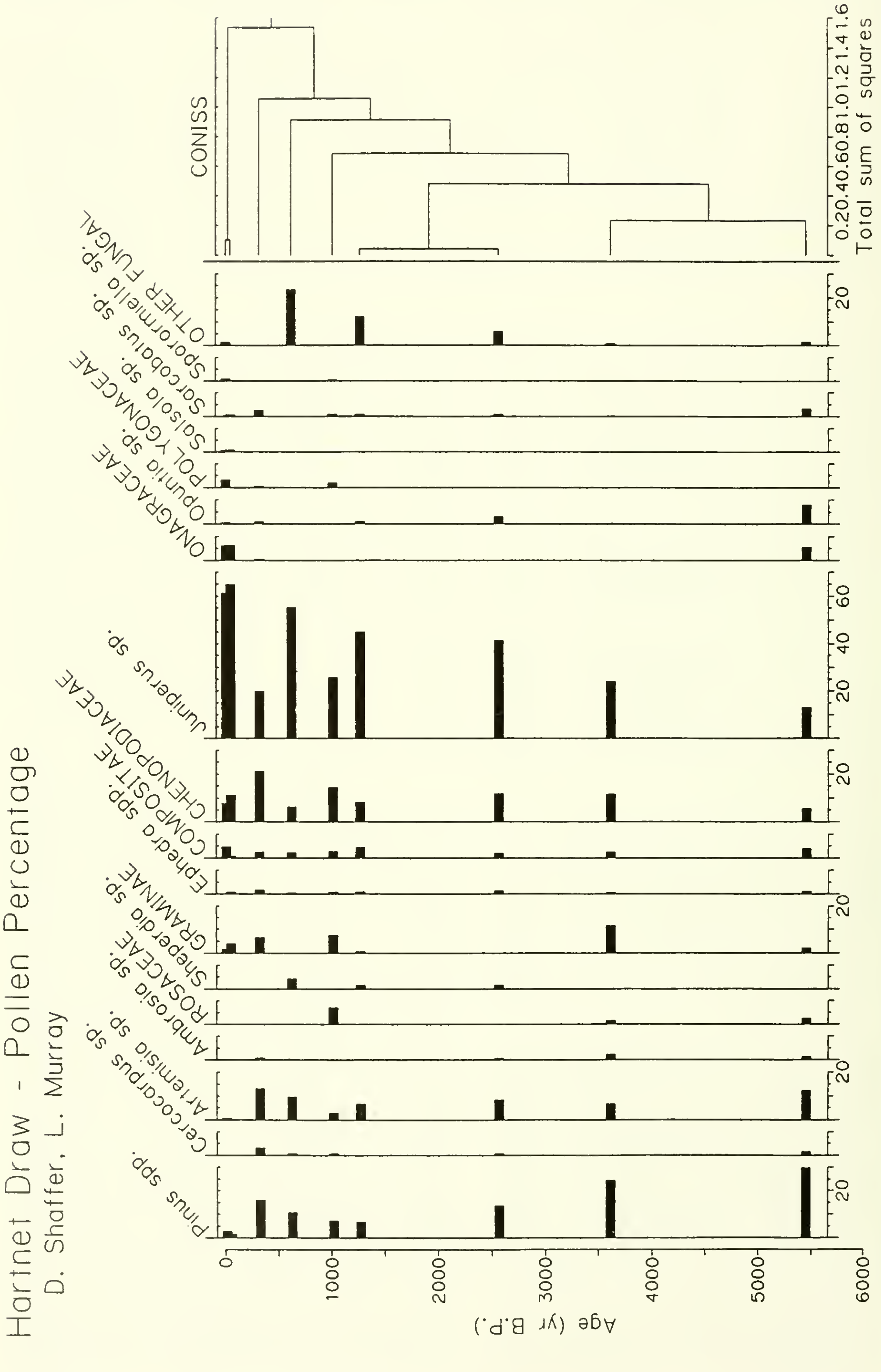

Fig. 4. Fossil pollen from Hartnet Draw packrat middens.

DISCUSSION

Figure 2 shows the site as it is now and a reconstructed image of how it may have looked prior to settlement. The reconstructed image shows greater coverage of grasses, winterfat, sagebrush, and pinyon inferred from the macrofossils and pollen found in the packrat middens. Although vegetation probably fluctuated continuously throughout the late Holocene, this midden record suggests that previous changes were minor compared to those of the last 200 yr. Sites similar in appearance to the reconstructed image are now present on ungrazed terraces that are inaccessible to large herbivores along Halls Creek, 90 km to the south (Heil et al. 1993). The presettlement plant community was undoubtedly more like the pinyon-juniper-grass community described by Heil et al. (1993) than the juniper-shrub community present at the site today.

It is clear from macrofossil and pollen analyses, reinforced by the 2 cluster analyses (Figs. 3, 4), that the modern midden plant contents are dramatically different from the presettlement middens. Furthermore, the presettlement middens are more similar to each other than to either of the modern middens. This suggests that the magnitude of change in vegetation during the last 200 yr was far greater than during the previous 5000 yr. Hypothetical causes of this vegetation change should account for both the timing of the change and the specific taxa that increased or decreased.

DROUGHT HISTORY.—Reductions in winterfat, pinyon pine, sagebrush, and ricegrass, and increases in juniper, rabbitbrush, and snakeweed might be attributed to droughts during the 19th or 20th centuries. However, an analysis of past drought frequency for southeastern Utah (Fig. 5) using 400 yr of tree-ring data compiled by Fritts (1991) suggests that droughts of the 19th century were not unusually severe when compared to the 17th century. Severe droughts, defined here as years with <165 mm of annual precipitation, reconstructed for Moab, Utah, occurred 9 times in the 17th century, 4 times in the 18th century, and 7 times in the 19th century. The 5 driest years, reconstructed from the tree-ring record, were A.D. 1667 (132 mm), 1684 (142 mm), 1668 (143 mm), 1879 (147 mm), and 1861 (150 mm). Exceptionally dry successive years were 1624–1626, 1666–1670, 1684–1685, 1728–1729, 1822–1823, 1879–1880, and 1899–1900.

Less is known about climatic variability in this region over the previous 5000 yr (prior to this tree-ring record), but it seems unlikely that any climatic event of the last 200 yr was sufficient to cause a change with no precedent during the previous 5000. Drought may have precipitated some of the dramatic vegetation changes of the last 200 yr, but it did not set the stage for them. This would require an event unprecedented during the previous 5000 yr.

FIRE HISTORY.—Some changes recorded in the middens could have been caused by changes in fire regime. The increase in juniper could have resulted from a decrease in fire frequency caused by elimination of grassy fuels by grazing. But this does little to explain the shift from palatable to nonpalatable species or the reductions of pinyon, sagebrush, and buffaloberry just at the time that fire frequency decreased. Fires of unprecedented severity could have been set during the settlement era, but this hypothesis has no data to support it. Studies of tree fire scars or sedimentary charcoal would have to be conducted to test this possibility.

GRAZING IMPACTS.—Impacts from introduced herbivores, especially large sheep herds in the late 19th and early 20th centuries, are the most likely cause of recent radical vegetation changes. The introduction of sheep, goats, cattle, and horses was without precedent during the previous 5000 yr. Overall, vegetation has shifted from palatable toward less palatable forage. Specifically, palatable grasses, winterfat, and buffaloberry decreased, while less palatable species, rabbitbrush, snakeweed, and greasewood, increased. Rabbitbrush and greasewood are poor forage, while snakeweed is typically an invader or increaser on overgrazed range (Benson and Darrow 1981, Heil et al. 1993, Cronquist et al. 1994).

Other studies conducted on grazing at Capitol Reef support this conclusion. Heil et al. (1993), in a survey of the vegetation of Capitol Reef National Park, suggest: "Some of the most preferred plant species (for grazers), e.g. *Ceratoides lanata* and *Stipa comata*, may have been locally extirpated by grazing." This packrat midden record demonstrates that, for the Hartnet Draw site, this was the case.

Additional research at Capitol Reef National Park indicates grazing has caused, and may

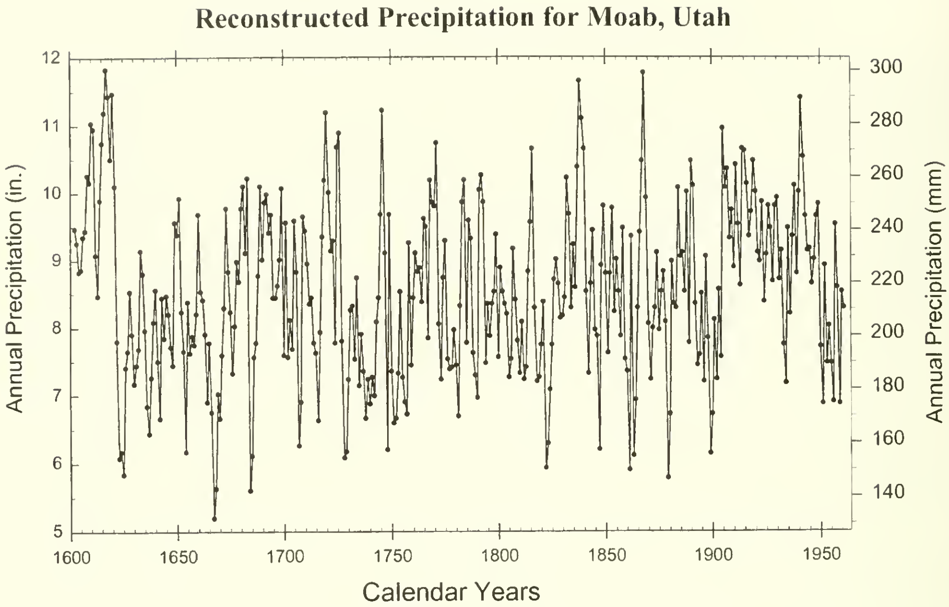

Fig. 5. Reconstruction of the last 400 yr of precipitation at Moab, Utah, from tree-ring data generated by a program distributed by Fritts (1991).

still be causing, changes to the natural habitat. Plant phytolith analysis in buried soil horizons shows a reduction of palatable grass species over the last several hundred years (Fisher et al. 1995). An analysis of riparian areas indicates that dramatic changes had occurred prior to the Taylor Grazing Act of 1934. Forage plants were heavily used, and in many instances cover was entirely removed. Recent grazing has perpetuated this removal or reduction of species and inhibited potential recovery (Barth and McCullough 1988). In a lightly grazed area palatable shrubs and grasses have increased significantly.

Dramatic declines in pinyon, sagebrush, and buffaloberry may also have been caused by the grazing history, but effects on these species are less well understood. These declines are also present in 14 additional middens from sites elsewhere in Capitol Reef National Park, such as along Hall's Creek (Murray 1989, Cole 1992).

Pinyon-juniper woodlands have reportedly increased during the historic period. This is especially evident when comparative photographic techniques are used (West et al. 1975, Tausch et al. 1981). This increase in pinyon-juniper woodlands is thought to be caused by reduced competition from grasses and forbs, which were eliminated by grazing and by consequent reductions in fire frequency. But studies discriminating between pinyon and juniper do not portray identical histories for both species. Pine and sagebrush both declined while juniper dramatically increased during the settlement period at Peck's Lake, Arizona (Davis 1987). A study of permanent plots in a presently ungrazed part of Pine Valley, Utah, demonstrated a significant decrease in juniper and significant increase in pinyon between 1933 and 1989 (Yorks et al. 1994). A study of tree-age structure on a presently ungrazed site in southwestern Utah's Needle Range found that during the 19th century many surviving juniper and few pinyon were established. By 1915 the situation had reversed, with far more surviving pinyon becoming established in this century (Tausch and West 1988). These results demonstrate that pinyon and juniper respond differently to changing regimes of grazing, fire, or climate. The observation that heavy grazing causes an expansion of pinyon-juniper woodland (West et al. 1975) does not equate with the expansion of both species in all habitats.

These results suggest that pinyon may be recovering now at some sites from a late 19th-century/early 20th-century decline caused by grazing impacts. This recovery has not yet occurred at Hartnet Draw. This hypothesis has support despite the lack of recent observations of pine removal by grazing cattle. Knowledge of the effects of cattle grazing at present stocking levels forms an inadequate basis for judging the effects of an overstocked sheep range during the droughts of the late 19th century. Although cattle will consume some pine when it is available (Pfister and Adams 1993), sheep readily consume pine needles and strip pine bark even in the absence of drought conditions (Anderson et al. 1985). Sheep accomplished the near complete elimination of the Bishop pine forest (*Pinus muricata*) on Santa Cruz Island, California, where they were not fenced out (Hobbs 1980).

Sagebrush populations may have a similar history despite observation of increases in sagebrush caused by the removal of their grass competitors (Young et al. 1978). Although sagebrush may be increasing on land presently grazed by cattle, this is not an appropriate analog for intense 19th-century sheep grazing. Sagebrush is consumed by sheep during droughts. During the late 19th century, sheep severely reduced populations of California sagebrush (*Artemisia californica*) on Santa Rosa Island, California, after first consuming the grass (Cole and Liu 1994).

MAGNITUDE OF CHANGE.—Recent vegetation changes recorded at Capitol Reef National Park are unique when compared to natural changes of the last 5000 yr. These results echo those of Davis et al. (1977), who found the vegetation change caused by domestic livestock reflected in fossil pollen at Wildcat Lake, Washington, to be greater than any other event of the last 1000 yr.

It is also possible that both climate and grazing combined to produce the dramatic vegetation shifts of the last 200 yr. There is little doubt that the most severe grazing damage occurs when high populations of herbivores compete for food during a severe drought. The droughts of 1879–1880 and 1899–1900 probably exacerbated damage caused by high herbivore populations. More severe earlier droughts, such as those during the 17th century, did not cause such changes because the large introduced herbivores were absent.

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MULE DEER AND PRONGHORN USE OF WASTEWATER PONDS IN A COLD DESERT

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ABSTRACT.—Pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) were counted at wastewater ponds at the Idaho National Engineering and Environmental Laboratory (INEEL) in southeastern Idaho 4 to 8 times per month from August 1989 through July 1991. Mule deer used wastewater ponds ($n = 15$) from June through December and were most commonly observed August through November. Pronghorn frequented wastewater ponds from May through November and were most common from July through September, the driest and warmest months; ponds were also used heavily in November 1990. Diel activity was studied from July through October. Mule deer use of ponds varied in relation to 8 diel time periods in August ($P = 0.02$) and September ($P = 0.01$) while pronghorn use varied by time period ($P < 0.01$) in all 4 months. Mule deer were more active at ponds during nocturnal than diurnal counts from July through September ($P < 0.01$). Pronghorn diurnal activity exceeded nocturnal activity ($P < 0.01$) August through October. Mule deer and pronghorn use of ponds was not related to distance from site facilities (groups of buildings used for research and other purposes). Pronghorn made greater use of individual ponds lacking additional nearby watering sites, and both pronghorn and mule deer were attracted to ponds with grass/forb and shrub cover around the upland periphery.

Key words: pronghorn, mule deer, desert, Idaho, diel activity, ponds, wastewater.

During warmer and drier periods of the year, mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) in desert habitats may seek free water (Beale and Smith 1970, Yoakum 1978, Hervert and Krausman 1986). Diel temperature patterns during warm and dry conditions may influence watering and activity patterns of mule deer (Eberhardt et al. 1984, Hervert and Krausman 1986) and potentially pronghorn (Deblinger and Alldredge 1991). Mule deer and pronghorn are found sympatrically on the Idaho National Engineering and Environmental Laboratory (INEEL), a Department of Energy research area located in the upper Snake River plain. In this semiarid environment ephemeral water sources are often available in the spring. Permanent watering sites on the 231,600-ha INEEL, however, are limited to a few game-watering cisterns, and sanitary, industrial, and radioactive wastewater ponds.

Concerns about mammal use of wastewater ponds stem from possible effects to the mammals (Halford and Markham 1978, Kuzo et al. 1978) and possible transport of contaminants to hunters (Reynolds and Rose 1978, Hoskinson and Tester 1980) if game mammals leave the INEEL. Studies thus far have shown that radiation does not pose a hazard to animals that directly use the ponds (Halford et al. 1982, Millard et al. 1990) or to secondary consumers (Markham and Autenrieth 1976, Arthur and Markham 1982).

Artificial systems such as INEEL wastewater ponds are becoming increasingly common in North America and many other regions of the world. The degree to which such ponds are used by large mammals and their potential influences, either negative or positive, have been largely overlooked. Our objectives were to evaluate wastewater ponds to (1) determine monthly and diel patterns of pond use by mule deer and pronghorn, and (2) determine characteristics associated with use or nonuse of ponds by mule deer and pronghorn.

STUDY AREA

The INEEL is located in southeastern Idaho and has an average elevation of 1485 m (Fig. 1). Temperatures range from –44°C to 39°C, with July normally the warmest month. Average daily temperatures range from –11°C to 21°C. Average annual precipitation is 21 cm. Typically,

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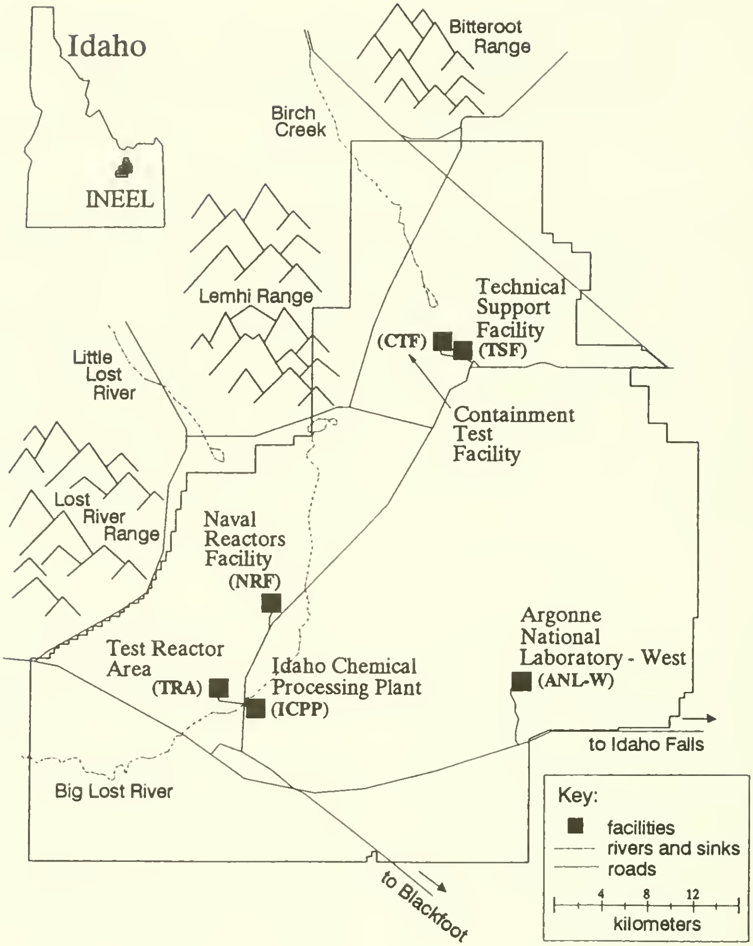
Idaho
INEEL
Bitteroot Range
Birch Creek
Lemhi Range
Little Lost River
Lost River Range
Technical Support Facility (TSF)
(CTF)
Containment Test Facility
Naval Reactors Facility (NRF)
Test Reactor Area (TRA)
Idaho Chemical Processing Plant (ICPP)
Argonne National Laboratory - West (ANL-W)
to Idaho Falls
Big Lost River
to Blackfoot
Key:
facilities
rivers and sinks
roads
4 8 12
kilometers

Fig. 1. Location of facilities at the Idaho National Engineering and Environmental Laboratory (INEEL) where wastewater ponds were surveyed for mule deer and pronghorn, August 1989–July 1991.

precipitation levels are highest in May and June and lowest in October. Relative humidity is commonly at its yearly minimum (daily average approximately 30%) in July and maximum (69%) from December through February (Clawson et al. 1989).

Most plant communities on the INEEL are dominated by desert shrubs, particularly Wyoming big sagebrush (*Artemisia tridentata wyomingensis;* Anderson et al. 1996). Other common shrubs are green rabbitbrush (*Chrysothamnus viscidiflorus*), gray rabbitbrush (*C. nauseosus*), winterfat (*Krasheninnikovia lanata*), and spiny hopsage (*Grayia spinosa*); assemblages dominated by shadscale (*Atriplex confertifolia*), Nuttall saltbush (*Atriplex falcata*), and winterfat, similar to salt-desert shrub communities, may occur on old lakebed sediment (Anderson et al. 1996). The primary native grasses include thick-spiked wheatgrass (*Elymus lanceolatus*), bottlebrush squirreltail (*E. elymoides*), Indian ricegrass (*Oryzopsis hymenoides)*, needle-and-thread grass (*Stipa comata*), and Nevada bluegrass (*Poa secunda;* Anderson et al. 1996).

Wastewater ponds at which mule deer and pronghorn were studied contained sanitary waste, industrial waste, radioactive waste, or a combination of waste types. Ponds were located on the periphery of groups of buildings (site facilities) being used for research, maintenance, operations management, and other purposes (Fig. 1). We eliminated 2 INEEL ponds from analysis because they were surrounded by a 3-m-high chain-link fence that excluded pronghorn and mule deer. Fifteen ponds were readily accessible to mule deer and 13 to pronghorn. Most ponds were rectangular and ranged in size from 0.02 to 2.21 ha. One additional wastewater source was a waste ditch that we included only in the monthly use and diel activity studies. Shorelines were gravel and subsoil, plastic-lined, or cobble over plastic-lined. Only 3 ponds contained emergent vegetation, and 1 other had abundant submerged vegetation. Ponds were partially to completely ice covered from late November through early March. Ponds are described in further detail by Cieminski (1993).

Birch Creek and Little Lost River at one time terminated in playas on and at the edge of the INEEL, respectively (Fig. 1). Most flow is now diverted for upstream irrigation of crops. Big Lost River flows onto the INEEL only in years following heavy snowfall, the last of which prior to our study was 1987. The ponds may, in small part, compensate for wetland habitat lost since surface water no longer flows regularly onto the INEEL.

METHODS

Counts of Mule Deer and Pronghorn

We conducted monthly diurnal and nocturnal counts on each pond, August 1989 through July 1991. The period from August 1989 through July 1990 was defined as year 1 when year was used in analyses; August 1990 through July 1991 was defined as year 2. Mule deer and pronghorn were considered to be at the pond site if they were within 100 m of a pond. We used a spotlight for nocturnal counts, which lasted about 15 min and were not conducted during inclement weather.

Five diurnal (sunrise through sunset) and 3 nocturnal (dusk through dawn) time periods, each 2 h long, were established during which counts were conducted from July through October. Time periods were sunrise (centered 0.5 h after sunrise), mid-morning, midday, mid-afternoon, sunset (centered 0.5 h before sunset), dusk (centered 1.5 h after sunset), midnight (centered around 2400 military time), and dawn (centered 1.5 h before sunrise). Diurnal and nocturnal counts from March through October were conducted in a manner that assured sampling of all ponds in all time periods. We attempted to visit a pond no more than once per 24-h period.

Due to shortened daylight hours and decreased activity around the frozen ponds, we reduced monthly surveys to 3 diurnal (sunrise, midday, and sunset) and 2 nocturnal (dusk and dawn) counts per month in November and December. In January and February 1990, counts were conducted as in November and December except only 1 nocturnal count (either dusk or dawn) was conducted. Ponds were not surveyed in January and February 1991 due to lack of target species observations during these months in 1990. Diurnal and nocturnal counts were rotated from November through February to assure sampling of all ponds during all time periods used in those months.

We attempted to initiate monthly diurnal and nocturnal counts about 30 d after initiation of counts in the preceding month. Ponds were scheduled to be counted only once per day because observer presence at the ponds could influence later pond counts. Monthly counts were conducted on consecutive days unless interrupted by inclement weather.

Monthly and Diel Use Analysis

"Observations" were used as an indication of pond use. For example, 2 pronghorn seen once or 1 pronghorn seen twice would both equal 2 observations. For monthly use for the entire year, we made data comparable between months by summing the number of observations in a month for year 1 and year 2 (at all ponds combined) and dividing by the number of counts conducted during that month (for both years combined). For example, the total number of pronghorn observed during diurnal periods at ponds in July of year 1 plus year 2 would be divided by the following denominator: 5 count periods per pond × number of ponds surveyed × 2 yr. Monthly data were then presented as the average number of pronghorn or mule deer observed per diurnal or nocturnal count.

For analysis of diel use patterns, we summed the number of target species observations in each year, month, and time period (8 diel time periods) over all study ponds. Using log-linear analysis under Categorical Data Modeling procedures (CATMOD; SAS Institute Inc. 1989a), we examined differences ($P < 0.05$) in diel use patterns. Diel activity was analyzed for differences due to diel time period and month for the period from July through October for year 1 and year 2. In a second analysis we compared diurnal use of ponds with nocturnal use, including month and time (diurnal or nocturnal) as explanatory variables in the logistic regression; in this analysis we also used the period from July through October. The sum of observations over the 5 diurnal time periods was compared with an adjusted sum of observations for the 3 nocturnal time periods. Nocturnal counts were adjusted to make them comparable with diurnal counts as follows: adjusted sum = mean observations per nocturnal count × 5.

Pond Characteristics

The number of ponds or ditches within a 1-km circle of a surveyed pond (from the pond center) was obtained from maps and aerial photos, as was the distance to site facilities. Shoreline distance (meters of shoreline/pond) was determined by superimposing sketches of water surface area and shoreline interface on blueprints of ponds or drawings made from direct measurements. Shoreline distance was remeasured whenever fluctuating water levels appeared to influence this measurement. During summer 1991 we determined percent cover of shrubs and grasses/forbs (combined) around the ponds by running six 20-m line-intercepts (evenly spaced and perpendicular to the shoreline) at each pond; plant coverage around ponds appeared to have changed little from 1989 through 1991. The method used was that described by Canfield (1941) except only 1 intercept line, placed 1 m off the ground, was used for both shrubs and grasses/forbs. Because of restricted access, we visually estimated vegetation coverage inside the fences around radioactive ponds ($n = 2$). Percentage of shoreline (from the water to 1 m onto the shore) lacking vegetation or with vegetation <15 cm tall was estimated and defined as bare shoreline. The vertical distance from the water surface to the top of the surrounding berm was defined as pond relief. We obtained weather data from a National Oceanic and Atmospheric Administration weather station located in the south central portion of the INEEL.

Mule deer and pronghorn occurrences at ponds were compared to pond characteristics from July through November. Each month ponds were grouped by target species into those with no pronghorn or mule deer observations and those where these target species were observed; months were then combined for the analysis. Thus, in the analysis a particular pond and its characteristics could fall into a different category each month, depending on target species observation data. We assumed that the target species were selecting ponds based on pond characteristics and location in relation to facilities and other ponds. Logistic regression (SAS Institute Inc. 1989b) was used to identify possible pond characteristics associated with use of ponds by target species. Logistic regression models were developed with a stepwise procedure at an alpha level of 0.05.

RESULTS AND DISCUSSION

Monthly Use

Mule deer first appeared at study ponds in June after a January through May absence (Fig. 2). In the intermountain region, June is the beginning of mule deer fawning season, which runs through mid-July (Robinette and Olsen 1944). Juveniles were first seen at the ponds in July but were not commonly seen until mid-August. Pond use by juveniles increased through the summer and fall to a peak (diurnal plus nocturnal) in November. Observations of adults steadily increased through the summer and early fall, then remained constant through November. Mule deer were not reported by age in December because we had increasing difficulty distinguishing between adults and juveniles under survey conditions.

Many mule deer are year-round residents on the INEEL but apparently are not dependent on ponds in the spring. Swank (1958) and Hervert and Krausman (1986) reported movements to water by mule deer in Arizona associated with increased temperatures; these movements may be associated with changing needs for water as metabolic rates increase and, at higher ambient temperatures (38°C), as evaporative cooling increases (Hervert and Krausman 1986). During these hot, dry periods, mule deer normally remain in their home range even if regular excursions are necessary to seek water (Hervert and Krausman 1986, Boroski and Mossman 1996). In our study the peak in mule deer observations in September lagged 2 months behind the temperature peak in July. July follows the 2 wettest months of the year on the INEEL; July through November is the driest series of months (Clawson et al. 1989). During our study precipitation in July was lower than in any other month (INEEL,

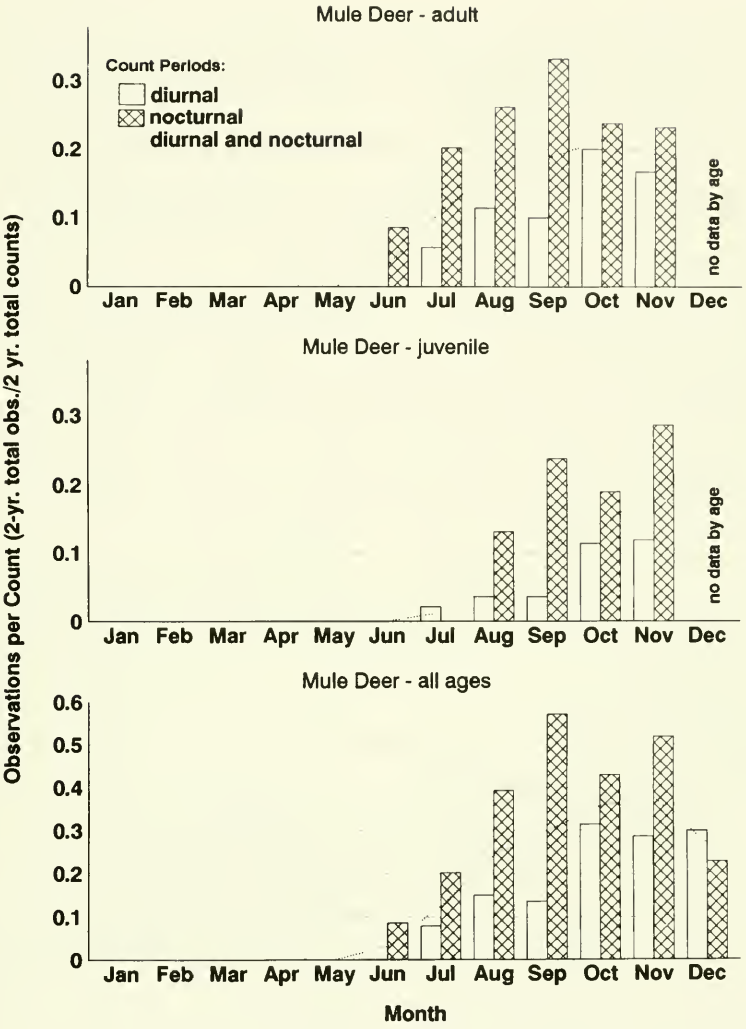

Fig. 2. Monthly use of wastewater ponds in southeastern Idaho by mule deer. Monthly use was calculated as the mean number of mule deer (observations) seen per visit to a pond (count), August 1989–July 1991; dotted line represents mean observations per visit for all 8 diel time periods.

National Oceanic and Atmospheric Administration unpublished data). This precipitation pattern and availability of forbs around pond edges may influence pond visitation patterns by mule deer on the INEEL.

Beale and Smith (1970) reported that highest water consumption by pronghorn in Utah varied from July to September, depending upon forage succulence (moisture content), which was dependent on precipitation. Pronghorn pond visitation in our study (Fig. 3) peaked in November. However, the November peak in adult and juvenile numbers was caused by several observations of large herds in November 1990; no pronghorn were seen in November 1989. Excluding November, adult pronghorn observations peaked in July through September and then declined in October (Fig. 3). Juvenile pronghorn were first seen at study ponds in June. Use by juvenile pronghorn then remained low through October with the same November peak (due to large herds in 1990) as in adults.

During colder months resident pronghorn on or near the INEEL are joined by pronghorn moving to lower altitudes (Hoskinson and Tester 1980). With the exception of November (from herds observed in 1990), pronghorn use of INEEL ponds during 1989 and 1990 generally declined after August or September. Lack

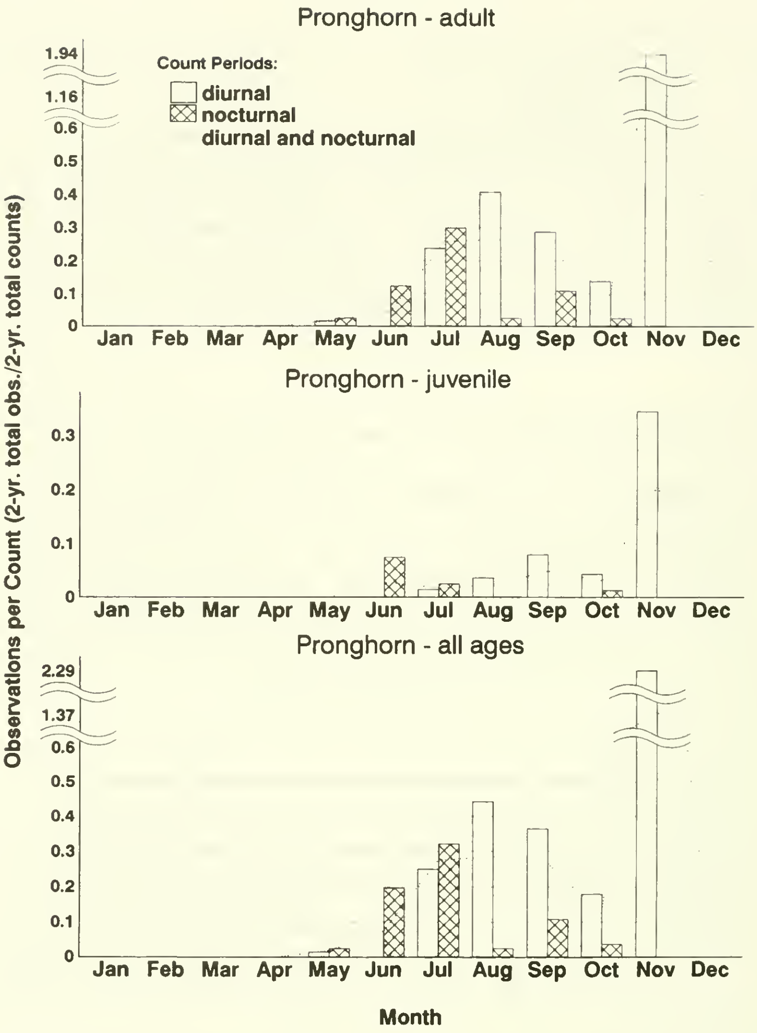

Fig. 3. Monthly use of wastewater ponds in southeastern Idaho by pronghorn. Monthly use was calculated as the mean number of pronghorn (observations) seen per visit to a pond (count), August 1989–July 1991; dotted line represents mean observations per visit for all 8 diel time periods.

of heat stress and availability of snow may have reduced or eliminated the need for drinking water during the cooler months. We cannot explain the later seasonal peak in pond observations of mule deer compared with pronghorn.

Although ponds were ice free by mid-March, we observed no pronghorn at ponds until May. During May and June, pronghorn dependence on INEEL ponds was also low because air temperatures were low, plant moisture content was high (Beale and Smith 1970), and temporary rain pools were plentiful. Pronghorn in Wyoming's Red Desert were attracted to free water during summer but did not move from an area when the water source was no longer available (Deblinger and Alldredge 1991); these authors note that moisture content of vegetation was high throughout the summers of their study and that these results may not apply to an unusually hot, dry summer.

Diel Use

Observations from the 8 diel time periods were used in analysis of diel pond use by target species from July through October of year 1 and year 2 (Figs. 4, 5). Both time period and month influenced ($P = 0.01$) numbers of mule deer observed at ponds (Fig. 4); there was a time period × month interaction ($P = 0.01$). When months were analyzed individually, time period had a significant influence on mule deer observations only in August ($P = 0.02$) and September ($P = 0.01$).

Log-linear analysis indicated that mule deer use of ponds was greater ($P = 0.01$) during the nocturnal (dusk to dawn) than diurnal (sunrise to sunset) portion of the diel cycle (Fig. 4); the analysis also indicated that months ($P = 0.01$) influenced our counts and that there was a month × time (nocturnal and diurnal) interaction ($P = 0.01$). When we examined months individually, mule deer were more likely ($P < 0.05$) to be at ponds during nocturnal periods in all months except October. In October of year 1, we observed mule deer only during daylight hours (Fig. 4).

Due to the small sample size, we did not separate antlered mule deer from adult females. The percentages of antlered adults were similar between diurnal (16.7% antlered) and nocturnal (17.3% antlered) surveys from July through October.

Among black-tailed deer (*O. h. columbianus*), Miller (1970) found differences in diurnal activity due to time in all months; morning and twilight peaks occurred June through September, early morning and midday peaks in October and November, and high use mid-morning till twilight in December. We observed considerable midday or mid-afternoon occurrence of mule deer at ponds in September and October but no strong sunrise or sunset peaks in activity during the diurnal cycle (Fig. 4). Interestingly, within the nocturnal period, deer were as active at ponds during midnight as during dusk and dawn. Hervert and Krausman (1986) suggested that desert mule deer does, during the warmer, drier months in Arizona, may have remained less active during the diurnal period to avoid water loss and to conserve energy. In general, diurnal activity in midsummer in our Idaho study was greater than that observed by Hervert and Krausman (1986), probably a result of milder daytime temperatures.

Numbers of pronghorn observed at ponds during the 8 diel time periods were related to time period ($P = 0.01$) and month ($P = 0.01$); there was a time period × month interaction ($P = 0.01$). Analysis by individual months indicated that time period had an effect ($P < 0.01$) on numbers of pronghorn observed at ponds in all 4 months; they were observed at ponds in all time periods except dawn (Fig. 5).

Pronghorn used ponds at different rates ($P = 0.01$) during the diurnal and nocturnal portions of the diel cycle; there was also a month effect ($P = 0.01$) and a time × month interaction ($P = 0.01$). When months were analyzed separately, pronghorn use of ponds was greater ($P < 0.01$) during daylight hours from August through October. Change in use due to time (diurnal and nocturnal) was not statistically significant ($P > 0.05$) in July. Greater diurnal use of ponds from August through October at the INEEL is similar to observations in Wyoming by Amstrup (1978). Nocturnal activity is consistent with observations that daytime activities are also engaged in at night, albeit generally at a lower frequency (Buechner 1950, Kitchen 1974, Amstrup 1978).

Amstrup (1978) observed crepuscular daily peaks of pronghorn activity July through November; Reynolds (1984) observed similar patterns in summer on the INEEL. Taylor (1972) recorded a midday peak June through August in Wyoming in pronghorn activity, in addition to crepuscular peaks. Peaks in activity from September through November were at 0600, 0900, and 1300 h (Taylor 1972). Our observations related to occurrence of pronghorn at ponds and not to general increases in activity. Still, pronghorn at ponds were actively feeding and watering and would have been rated as active by other authors. Pronghorn use of wastewater ponds was irregular for diel time periods from July through October in our study (Fig. 5); there was no strong trend of increased use of ponds in crepuscular hours.

Use in Relation to Pond Characteristics

Fifteen ponds were accessible to mule deer on the INEEL and 13 to pronghorn. The 2 ponds used by mule deer but not by pronghorn lacked an open gate and were surrounded by mesh wire plus barbed wire on the top that mule deer readily jumped. In addition to wastewater ponds, mule deer and pronghorn frequently used a wastewater ditch that extended for over 1000 m across the shrub desert. During the period from July through November, mule deer were observed at 12 of 15 available study ponds. Pronghorn were observed at 10 of 13 ponds accessible to them.

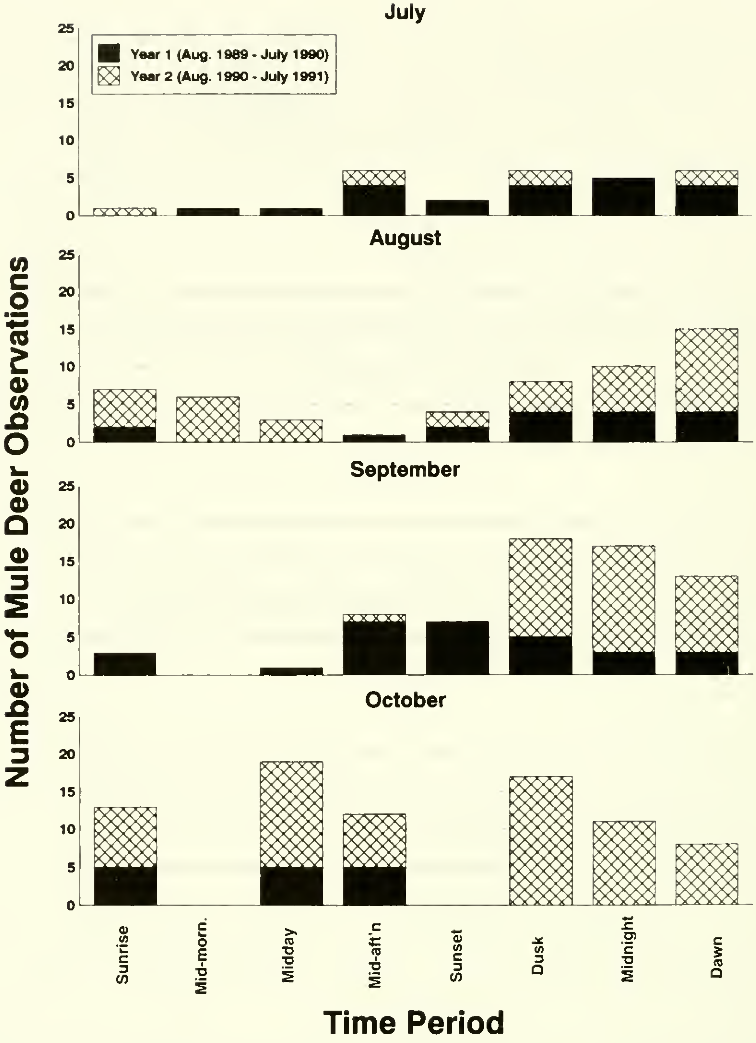

Fig. 4. Diel use (stacked bar graph, nonoverlapping patterns) of wastewater ponds in southeastern Idaho by mule deer. Diel use was calculated as the sum of mule deer seen at all ponds (each pond counted once during each time period within a month and year).

Differences in habitat variables between observation categories (mule deer observed or not observed) were found only for percent bare shoreline and percent grass/forb cover within 20 m of the pond (log-linear analysis; Table 1). Buildings and other physical facilities had no apparent influence on mule deer use of ponds. Logistic regression, using these 2 variables, identified percent grass/forb within 20 m of the ponds as the only significant variable separating observation categories ($P = 0.01$). Concordant pairs (61.9%) indicated that this is not a particularly strong logistic regression model.

We suspect that greater amounts of vegetation in the upland periphery next to the pond (percent shrubs was nearly significant) attracted mule deer to ponds either because of forage value or increased concealment. Ponds surrounded by bare soil (or subsoil) and gravel on the uplands looked much less natural and were apparently less attractive to mule deer.

For pronghorn, log-linear analysis using single variables indicated that all habitat variables other than distance to facilities were significantly different ($P < 0.05$) between pond observation categories (Table 1). When these variables

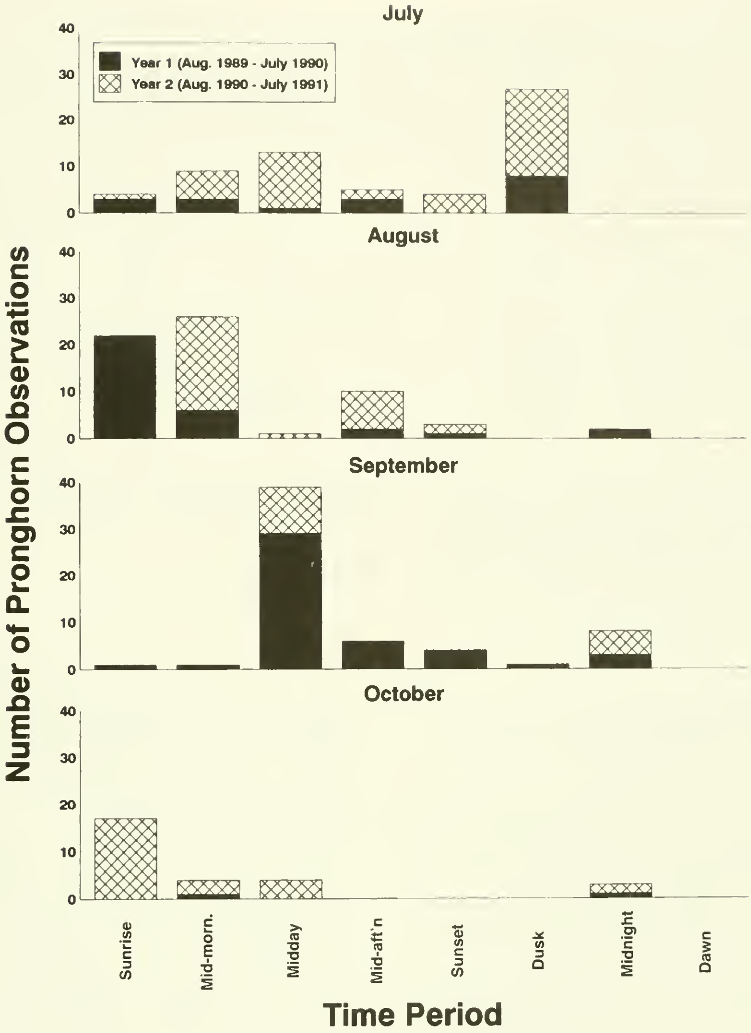

Fig. 5. Diel use (stacked bar graph, nonoverlapping patterns) of wastewater ponds in southeastern Idaho by pronghorn. Diel use was calculated as the sum of pronghorn seen at all ponds (each pond counted once during each time period within a month and year).

were evaluated as a group in logistic regression, only number of ponds within 1 km entered the equation ($P = 0.01$); as with mule deer, concordant pairs (63.0%) indicated that the model separating observation categories was not strong.

Increased isolation of ponds (fewer ponds within 1 km) was apparently associated with concentration of pronghorn use at a single pond. Other variables such as shoreline distance and percent shrub cover could also be used to develop a logistic regression model. Larger ponds were associated with increased chances of observing pronghorn. Both percent shrub cover and percent grass/shrub cover were associated with increased use of ponds by pronghorn.

We commonly observed pronghorn drinking water from some (usually larger) ponds. At smaller ponds pronghorn were flushed by observers' arrival, and we rarely saw them actually drinking. Pronghorn were also observed drinking from sources such as parking lot runoff catchments, guzzlers, road construction ponds, and leaks in piping to construction or maintenance work areas. These temporary water sources, quickly discovered by pronghorn, were

TABLE 1. Wastewater pond characteristics [median, mean ( )] and association (logistic regression by single variables) with occurrence[a] of target species at ponds from July through October.

Pond observation category	Shoreline distance (m)	% bare shoreline[b]	Pond relief[c] (m)	Ponds[d] <1 km	Distance to facilities (m)	% cover grass/ forbs	% cover shrubs
MULE DEER							
Not observed	195	100	1.8	3	82	5.1	1.4
($n = 100$)	(291.1)	(81.5)	(1.9)	(2.8)	(93.7)	(12.1)	(7.5)
Observed	392	80	1.7	3	52	17.8	9.1
($n = 30$)	(361.9)	(64)	(1.9)	(3.1)	(72.6)	(23.3)	(11.5)
$P >$ chi sq.	0.07	0.01	0.99	0.23	0.14	0.01	0.07
PRONGHORN							
Not observed	156.2	100	1.5	3	59	3	0
($n = 84$)	(248.9)	(85.2)	(1.8)	(3.0)	(80.02)	(13.3)	(3.94)
Observed	434	94.5	1.8	1	82	18	9.9
($n = 26$)	(363.4)	(69)	(2.2)	(1.96)	(91.6)	(21.8)	(11.9)
$P >$ chi sq.	0.01	0.03	0.01	0.01	0.42	0.03	0.01

[a] Each month on the INEEL from July through October wastewater ponds accessible to mule deer and pronghorn were grouped into those with target species and those without. Eight months (August–October 1989, July–October 1990, July 1991) were combined for the entire study for analysis.

[b] Percent bare shoreline is the percentage of a pond shoreline where vegetation is absent or <15 cm in height within 1 m of the land-water interface.

[c] Pond relief is the distance from the water to the top of the surrounding berm.

[d] Ponds within 1 km include any ponds or ditches, including the observation pond, that are available and have water for target species use.

probably selected over ponds if they were nearer the pronghorn's center of activity. However, none of these aforementioned water sources were permanent, and some lasted little more than a day.

Beale and Smith (1970) observed that pronghorn did not drink available water when moisture content of forbs was ≥75%; when moisture content in forage plants was insufficient, pronghorn regularly drank water. Reynolds (1984) found open water was within only 1 of the 5 home ranges of pronghorn bands studied at the INEEL. Pronghorn probably drink water if available and otherwise depend on moisture from vegetation consumed (Einarson 1948).

It was not unusual to see pronghorn feeding in the vicinity of a pond for a few minutes after drinking, probably an attraction to herbaceous vegetation around some of the INEEL ponds. Several authors have found that pronghorn use was greater in areas of higher soil moisture (Good and Crawford 1978), or that pronghorn selection of forage was influenced by succulence (Beale and Smith 1970). Forbs common at some study ponds that can be important in pronghorn diets were prostrate knotweed (*Polygonum aviculare*), dock (*Rumex* spp.), and poverty sumpweed (*Iva axillaris;* Ferrel and Leach 1950, Bruns 1977, Good and Crawford 1978). Of the 5 INEEL ponds with well-vegetated shorelines, 3 had the highest pronghorn use of all ponds, and 1 had intermediate pronghorn use. Vegetation around these ponds included willow-leaved dock (*R. salicifolius;* at all 5 well-vegetated ponds), prostrate knotweed (at 1 of the highest use ponds), and poverty sumpweed (at another of the highest use ponds).

Mule deer and pronghorn readily use wastewater ponds at the INEEL, perhaps as much for the surrounding succulent vegetation as the drinking water. The presence of drinking water may be important to both species during the warmest and driest months of the year, particularly during unusually hot and dry years. Where ponds are determined to be safe for wildlife use, designs that include grass, forb, and shrub cover around wetlands would likely improve use by mule deer and pronghorn.

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OBSERVATIONS ON THE REPRODUCTION, SOURCES OF MORTALITY, AND DIET OF THE KENDALL WARM SPRINGS DACE

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ABSTRACT.—The life history of the endangered Kendall Warm Springs dace (*Rhinichthys osculus thermalis*) is largely unknown. Our study of its reproduction, sources of mortality, and diet indicated that Kendall Warm Springs dace seem to be reproductively active throughout the year, but the rate of reproduction appears to decrease during the winter. Males become sexually mature at 34 mm total length and females at 40 mm total length. We observed 2 sources of mortality: (1) emigration from the warm spring stream over a waterfall into the Green River and (2) predation on larvae by dragonfly (*Libellula saturata*) nymphs. Stomachs of Kendall Warm Springs dace contained small (≤1.5 mm total length) benthic invertebrates, primarily dipterans and mollusks.

Key words: Kendall Warm Springs dace, Rhinichthys osculus thermalis, *reproduction, mortality, diet.*

The Kendall Warm Springs dace (*Rhinichthys osculus thermalis*) is endemic to a single spring creek. Because of its restricted habitat, it has been listed as an endangered species, and a recovery plan has been developed that requires a more thorough description of its life history (U.S. Fish and Wildlife Service 1982). Hubbs and Khune (1937) and Binns (1978) made limited life history observations of the fish, but most aspects of its life history are poorly understood, including reproduction, sources of mortality, and diet.

STUDY AREA

Kendall Warm Springs Creek originates from several thermal springs (29.5°C) in a small limestone bluff 50 km north-northwest of Pinedale, Wyoming (Hubbs and Khune 1937, Binns 1978, Breckenridge and Hinckley 1978). The creek has a discharge of 2.0–2.5 m^3/s and courses for 340 m before cascading over a 4-m-high waterfall into the Green River. This waterfall prevents Green River fish from entering the spring creek. The creek has a mean depth of 10.6 cm, mean wetted width of 8.6 m, mean water velocity of 25 cm/s at the bottom, and a substrate composed mostly of a mix of fine (0.1–3.2 cm) and coarse (3.3–7.6 cm) limestone pebbles (Gryska 1996). Water flows through a braided network of channels among large vegetation mats (largely *Chara* spp.).

METHODS

During June, July, and August 1995, and January, May, June, and July 1996, we captured fish in traps in Kendall Warm Springs Creek. Traps were constructed of 3-mm-square-mesh hardware cloth. Measuring 5.5 × 11 × 31 cm, with a fusiform shape when viewed from the side, the traps had a V-shaped mouth with a vertical slot entrance. Traps were set in the main channel, secondary channels, and vegetated mats over the length of the spring creek during day and night (see Gryska 1996 for a detailed description of traps and sampling protocols). Gender and spawning condition were determined from external morphology and by manually extruding semen or ova. Sexually mature males were also identified by the presence of minute nuptial tubercles on the forehead, dorsal surface, and fins, and a longer (than immature males), whitish anal papilla. We did not observe the purple coloration reported in spawning males described by Hubbs and Khune (1937). Females were identified by the absence of nuptial tubercles, a larger (than immature females), clear anal papilla. Females were considered to be in spawning condition if they had a distended abdomen and eggs could be extruded by gentle pressure to the abdomen. Gender and total length (TL, mm) of captured fish judged to be in spawning condition were recorded.

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Observations of the presence of larval fish (6–15 mm TL) were made June through August 1994, and January and May through July 1995. During each sampling month we made visual observations with the aid of a powerful light between 2200 and 2400 h during at least a 5-d period by walking along each bank of the stream. We searched shoreline habitat that was 1–5 cm deep, without measurable current, and vegetated by *Chara* spp.

We observed a dragonfly (*Libellula saturata*) nymph in association with larval fish in shallow (<5 cm deep), slow-moving, near-shore habitat. To assess the density of dragonfly nymphs and larval fish, we randomly selected 10 sampling sites 2.0 m long and 0.6 m away from the bank where larval fish were observed. Thirty quadrats (0.02 × 0.02 m) were identified within each site. Each site was sampled 5 nights, 7–14 June 1995, between 2200 and 2400 h. Using a powerful light, we counted dragonfly nymphs and larval fish and observed the predatory behavior of dragonfly nymphs. The light did not appear to affect the behavior of either dragonfly nymphs or larval fish. Dragonfly nymphs and larval fish were counted in 3 randomly selected quadrats within each site.

The number of fish emigrating downstream out of Kendall Warm Springs Creek was estimated using two 0.4-m-diameter (500-micron-mesh openings) drift nets set at 2 points at the upstream edge of the cascade. Due to greater channel slope and current velocity (>1 m/s) at this location, fish collected there were being carried over the waterfall when captured. Nets were set horizontal to each other on a transect across the creek so that each net sampled a unique portion of the flow. Nets were set daily for 24-h periods between 22 July and 22 August 1994, 5 and 10 January 1995, and 25 May and 23 July 1995. Each drift net occupied 3.9% of the total stream width (10.4 m) at the falls. Traps were set and retrieved between 1000 and 1100 h. Fish were measured to the nearest millimeter (TL) and identified as larvae (<16 mm TL) or post-larvae (≥16 mm TL). Total number of fish emigrating daily over the falls was calculated by dividing the mean number of fish captured per 24-h net set by the proportion of total stream width (0.078) sampled with the 2 nets.

Trapping mortalities and fish caught in drift nets immediately upstream from the cascade were preserved in 70% ethanol and their stomach contents analyzed. The abdominal cavity of fish >20 cm TL was injected with a 70% ethanol solution to preserve stomach contents. In the lab we removed the stomach of each specimen and pooled the contents into 4 classes: (1) fish <40 mm TL captured during January 1995, (2) fish ≥40 mm TL captured during January 1995, (3) fish <40 mm TL captured May, June, or July 1995, and (4) fish ≥40 mm TL captured May, June, or July 1995. This enabled a comparison of food items between winter and summer and between 2 length classes, but it did not allow for assessment of variation among individual fish. Invertebrates in each identifiable taxon were enumerated by the Bureau of Land Management Aquatic Ecosystem Laboratory, Logan, Utah.

RESULTS

A total of 22,942 juvenile and adult fish were sampled with traps during the study. During each sampling month (January, May, June, July, and August) several fish were examined for the presence of semen or ova. Measurements of the lengths of individual fish with and without semen or ova could not be made because of the potential mortality associated with handling. The minimum length at which semen or ova could be extruded differed by gender. For males the minimum length at which semen could be extruded was 34 mm TL, whereas the shortest length at which ripe eggs could be extruded from females was 40 mm TL. Semen and ova could be extruded from males and females during all sampling months.

Larval fish were also observed during all sampling months. Mean densities in June were 2.8 larvae/0.04-m^2 quadrat, and larval fish were observed in 67% of the sampled (n = 150) quadrats. Estimates of densities of larval fish were not made using the sampling protocol outside of July 1995; however, visual observations along the shoreline indicated that densities were similar from May through August but substantially lower in January.

A total of 453 fish (329 larvae) were captured in drift nets at the upstream edge of the waterfall. From May through August average capture per 24-h sampling period was 3.96 ($s_{\bar{x}} = 0.35$) fish, including 2.90 ($s_{\bar{x}} = 0.34$) larvae in each of the 2 nets. We estimated that 100 (95% C.I. 85–120) fish emigrated from the stream each day (May–August), 75 of which were larval fish. Catch rates were substantially lower in January, averaging 0.81 fish, including 0.09 larvae, in each net per 24-h sampling period.

Dragonfly nymphs were 10–25 mm long and larval fish were <16 mm TL. Estimated density of dragonfly nymphs in larval fish habitat was 22.5 nymphs/m^2 ($s_{\bar{x}} = 2.25$; $n = 138$). Dragonfly nymphs were frequently observed either grasping or attempting to grasp larval fish, but no records of capture rates were obtained.

Many fish collected in traps had died and were in a state of decomposition, thus rendering them unsuitable for stomach content analysis; some fish had empty stomachs. Two fish ≥40 mm TL sampled in January had food items in their stomachs, and only 3 *Physella*, 4 *Hydracarina*, and 1 Chironomidae were found (Table 1). Two fish <40 mm TL sampled in January contained Chironomidae, *Optioservus*, *Physella*, and *Hyallela* (Table 1). During summer 32 fish ≥40 mm TL had Orthocladiinae and Planorbidae as the most common taxa (Table 1), and 38 fish <40 mm TL had predominantly riffle beetles (Elmidae), Chironomidae, *Physella*, Planorbidae, *Hyallela*, and *Simulium* in their stomachs (Table 1). Prey of Kendall Warm Springs dace were all ≤1.5 mm in length.

DISCUSSION

Our observations of Kendall Warm Springs dace and the work by Binns (1978) indicate that breeding occurs year-round. Males and females were observed in spawning condition and larval fish were observed during each sampling month (January, May, June, July, and August), indicating that the Kendall Warm Springs dace is reproductively active throughout the year.

We found evidence that reproduction decreases during winter. Very few larval fish were seen along the shoreline, and the number of drifting larvae was substantially less in January (0.09 larvae/24-h net set) than in May through August (2.90 larvae/24-h net set). Additionally, Gryska (1996) captured significantly fewer juvenile and adult fish in traps during winter than during summer, and mean length of fish captured in January was significantly greater than in summer. We submit 2 potential reasons for the decline: (1) an overall reduction in primary productivity due to shorter days and reduced intensity of sunlight, and (2) cooler water temperatures in shallow, near-shore larval fish habitat during the winter. Gryska (1996) measured water temperatures as low as 10°C in near-shore habitats in January 1995. Kaya (1991) was unable to stimulate spawning by *R. o. thermalis* in laboratory aquaria by varying photoperiod, water temperature, or current. Our observations suggest that photoperiod and/or water temperature influence reproductive rates.

Minimum length at sexual maturity was 34 mm TL for males and 40 mm TL for females. John (1963) found female speckled dace in Arizona to mature at age 2 and 45 mm standard length (SL). Kendall Warm Springs dace of 45 mm SL were 54 mm TL; they may mature at a smaller size compared to other speckled dace subspecies. Our longest captured Kendall Warm Springs dace was 63 mm TL (see Gryska 1996 for length frequency data).

Kendall Warm Springs dace regularly drifted out of the creek into the Green River during all sampling months (January, May, July, and August), and 75% of the drifting fish were larvae. Because larval fish are relatively poor swimmers, they are easily displaced downstream by the current. Larger fish found in the nets were often partly decomposed, and we suspect they may have been dead upon entrance. We probably underestimated the mean number of fish captured per 24-h period because larval fish were difficult to see and were often torn apart either by water flowing through the nets or by dragonfly nymphs captured in the nets.

We estimate that 75 larval fish per day drifted from the creek into the Green River from May through August (a total of about 9200 fish). Average larval fish densities were 2.8 larvae/0.04-m^2 quadrat, and larval fish habitat occupied 17% (329 m^2) of the creek (Gryska 1996). Given the density of larval fish and the area of larval fish habitat, we estimate the population to be about 24,000 larval fish in June, but the actual population was probably higher because it is unlikely that all larval fish were observed in each sampled quadrat. Given these

TABLE 1. Numbers of organisms found in the stomachs of 2 length classes (mm) of Kendall Warm Springs dace collected during winter (January) and summer (May–July) 1995. Number of fish stomachs pooled to form the sample is in parentheses.

		Winter		Summer	
Taxon	Life stage	<40 (2)	≥ 40 (2)	<40 (38)	≥ 40 (32)
Amphipoda, *Hyallela*	adult	6		3	
Hydracarina	adult		4	1	
Elmidae, *Optioservus*	larval			22	
Chironomidae	pupal	23	1	6	
Orthocladiinae	larval	1		1	87
Simuliidae, *Simulium*	larval			3	
Stratiomyidae	larval			2	
Hemiptera	adult			1	
Odonata, Libellulidae	larval			1	
Trichoptera	pupal			1	
Hydropsychidae, *Cheumatopsyche*	larval	1			
Hydroptilidae	larval	1			
Physidae, *Physella*	adult	19	3	4	1
Planorbidae	adult	1		4	9

estimates, it appears that the drift of larval fish from the stream may represent a substantial segment of the larval fish population. However, because reproduction appears to occur throughout the year, our estimates of larval fish abundance should be considered minimal estimates.

We estimate that 25 juvenile and adult fish per day drifted from the creek into the Green River from May through August (a total of about 3000 fish). We have no estimates of density of juvenile and adult fish, but a total of 22,942 fish were captured with 867 trap sets during summer 1994. Traps were set at least 4 m apart over the length of Kendall Warm Springs Creek, so only a portion of the population in the creek was sampled at one time. It seems unlikely that drift of juveniles and adults from the creek into the Green River causes a substantial loss from the population.

Dragonfly nymphs preying on larvae and small juveniles (<20 mm TL) contribute to mortality among Kendall Warm Springs dace, but the extent of the mortality is unknown. In addition to dragonfly nymphs, a number of other potential predators were observed along Kendall Warm Springs Creek during our study: dippers (*Cinclus mexicana*), Brewer's Blackbirds (*Euphagus cyanocephalus*), Great Blue Herons (*Ardea herodias*), and wandering garter snakes (*Thamnophis elegans vagrans*).

Kendall Warm Springs dace diet had not been reported previously. Our stomach analysis indicates they feed on epibenthic and epiphytic organisms, consuming small (≤1.5 mm total length) benthic invertebrates, particularly dipterans, riffle beetles (Elmidae), mollusks, amphipods (*Hyallela*), and water mites (Hydracarina). This is similar to other speckled dace that suck and scrape invertebrates from the substrate by using a subterminal mouth specifically adapted for benthic foraging (Baltz et al., 1982, Van Eimeren 1988). Although feeding behavior has not been recorded for speckled dace, other species of *Rhinichthys* have been observed feeding between and under rocks and on the upper and downstream surfaces of rocks (Gibbons and Gee 1972). Diets of other speckled dace subspecies have included Diptera, Ephemeroptera, Gastropoda, Coleoptera, water mites, and algae (Baker 1967, Li and Moyle 1976, Van Eimeren 1988). It appears that Kendall Warm Springs dace feed on items also utilized by other *Rhinichthys* species (Gibbons and Gee 1972, Reed and Moulton 1973, Brazo et al. 1978). Sample sizes were small because no fish could be sacrificed; only incidental mortalities in traps and fish captured in drift nets at the waterfall into the Green River were available for stomach analysis. Diet data we obtained are limited because stomach contents were pooled within seasons and length classes (<40 and ≥40 mm TL), and substantial digestion and deterioration of stomach contents were common because samples largely comprised fish that had died in traps or were captured in drift 12–24 h prior to being collected and preserved. Additionally, it is not known where the fish captured in drift nets resided previously in the creek. Consequently, fish stomach contents that we analyzed may not fully represent the diet of Kendall Warm Springs dace.

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TWO NEW SPECIES OF CHLOROPERLIDAE (PLECOPTERA) FROM CALIFORNIA

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ABSTRACT.—*Suwallia sierra* and *Sweltsa pisteri* are described as new species in the family Chloroperlidae from California, USA. Illustrations of the male terminalia of both species and the female and egg of *S. sierra* are presented. In addition, detailed figures of the epiproct of 2 similar species, *Sweltsa townesi* and *Sweltsa resima*, are included. Diagnoses are provided comparing the new taxa with related species. Observations indicate that *S. sierra* may belong to the same clade as the genus *Neaviperla*.

Key words: stoneflies, Plecoptera, Suwallia, Sweltsa, *Chloroperlidae, California.*

The stonefly fauna of California was first treated as an entity by Jewett (1960), who included 14 species in the family Chloroperlidae and gave limited distributional data and a key. Stark et al. (1986) listed 23 species for the state. Then Surdick (1995) named 2 additional species from California to bring the total to 25 chloroperlids.

We discovered 2 additional undescribed species of Chloroperlidae from California and decided to name them so they could be added to the growing knowledge of California stoneflies.

Suwallia sierra, new species

Figs 1–5, 13

MALE.—Macropterous. Body length 5–7 mm; forewing length 6–7 mm. General body color medium brown. Dorsum of head with dark brown interocellar area and Y-line. Mouthparts lightly sclerotized. Pronotum with margins and rugosities dark brown, disks light, angles rounded. Meso- and metanota with dark U-marks. Wings light with dark veins. Abdomen with dark brown median stripe on dorsum of segments 1–8, dark brown lateral marks on segments 1–2; tergum 9 with dense setal patches, posterior margin slightly excavated medially, not projecting posteriorly or heavily sclerotized. Hemitergal lobes very short, pointed; not attenuated into medially directed digitate processes (Fig. 3). Epiproct tip a small membraneous knob densely covered with fine curved setae; basal anchor, bar, and paragenital plates fused to form star-shaped plate; basal plate with small median dome and 15–25 stout setae on anterior 1/3, anterior margin of basal plate uneven and turned dorsally (Fig. 3). Aedeagus tubular, terminating in 2 apical lobes and 2 lateral lobes; subapical frontal surface with 2 curved sclerotized patches laterally, separated by 3 scaled lobes; proximal surface inflated and covered with fine spinules and scales (Figs. 1, 2). Cerci curved in basal segments 1–4; segment 1 elongated (length 2.5–4 times width), the posterior 1/4–1/3 slightly demarked from the anterior portion but lacking the free articulation of a separate segment; segments 2–4 (length = width) and posterior portion of segment 1 with stout spines on interior surface; remaining segments slender, straight, and lacking stout spines (Fig. 3).

FEMALE.—Macropterous. Body length 6–8 mm; forewing length 6–8 mm. General body color and external morphology similar to male. Subgenital plate wide at base, narrowing to median truncate, swollen lobe that protrudes at least 1/2 over sternum 9, plate originates near middle of sternum 8. Cercal segment 1 less elongated (length 2 times width) than on male, segments 1–4 not curved and lacking stout spines on interior surface (Figs. 4, 5).

NYMPH.—Body length 6–8 mm. General body color golden brown. Lacinia with main terminal tooth and small subapical tooth; double row of marginal setae: 20–24 equal-spaced setae on dorsal margin (12 stout, 4 medium, 8 fine), 16–18 setae on ventral margin (10 stout

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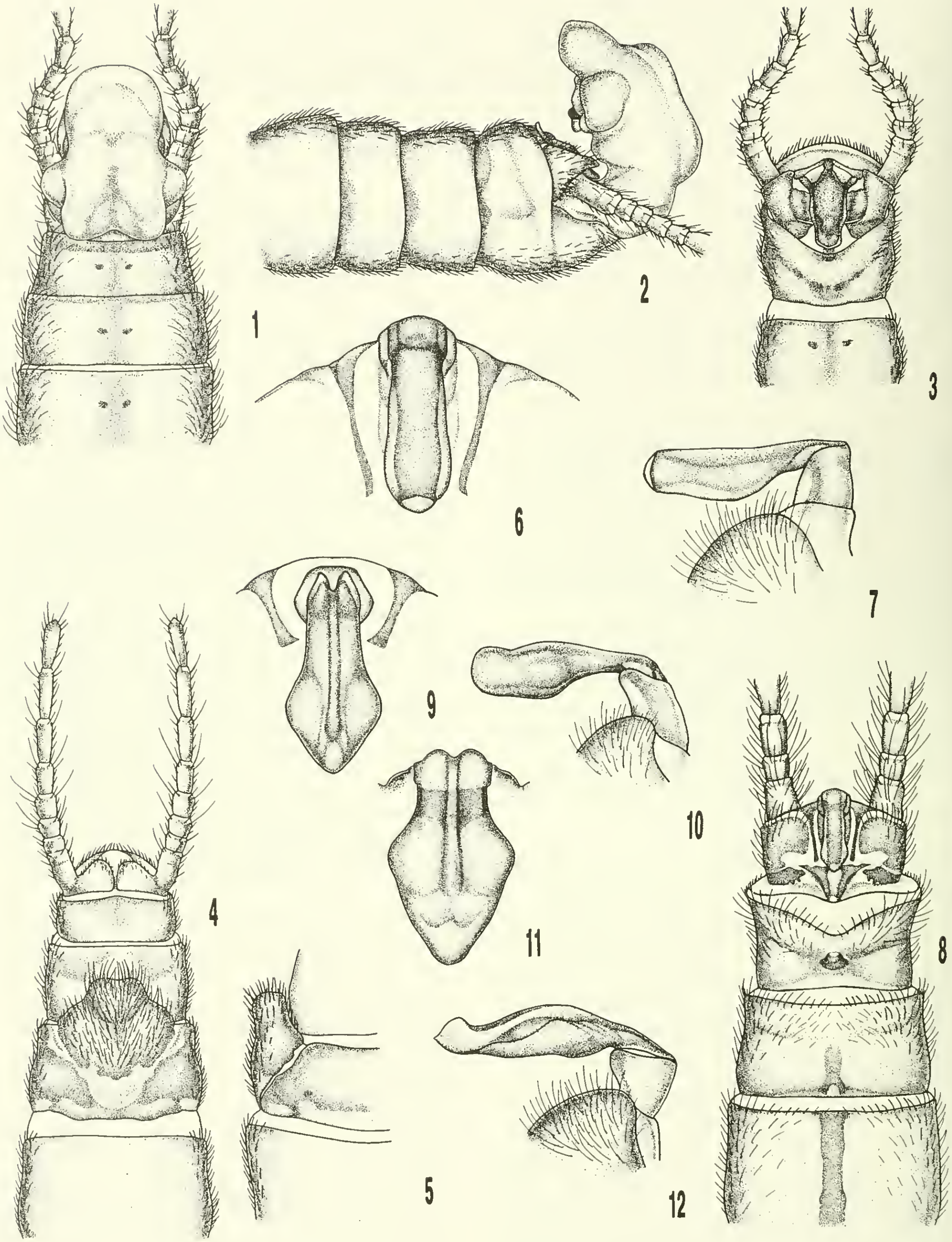

Figs. 1–5. *Suwallia sierra*: 1, male terminalia and aedeagus, dorsal; 2, male terminalia and aedeagus, lateral; 3, male terminalia, dorsal; 4, female terminalia, ventral; 5 female subgenital plate, lateral. Figs. 6–8. *Sweltsa pisteri*: 6, male epiproct, dorsal; 7, male epiproct, lateral; 8, male terminalia, dorsal. Figs. 9–10. *Sweltsa townesi*: 9, male epiproct, dorsal; 10, male epiproct, lateral. Figs. 11–12. *Sweltsa resima*: 11, male epiproct, dorsal; 12, male epiproct, lateral.

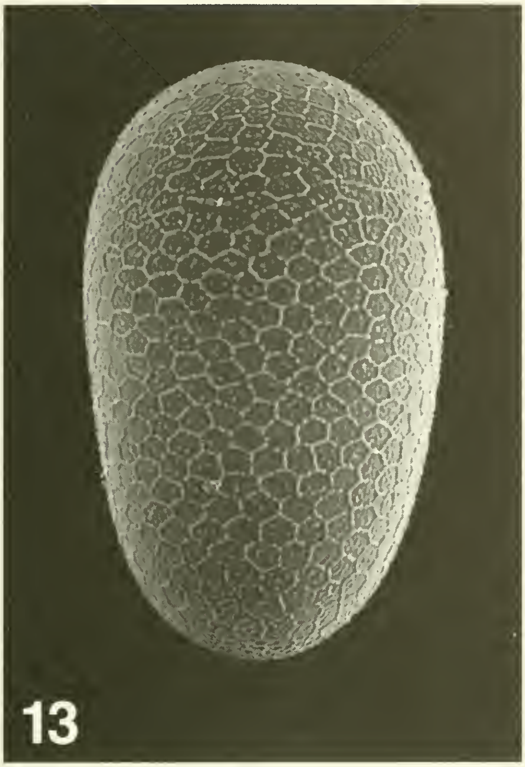

Fig. 13. *Suwallia sierra*: egg, lateral view (200X). California, Sacramento Co., small south bank tributary to Cosumnes River, upstream of Michigan Bar bridge, 29-IV-1996, R.L. Bottorff.

near subapical tooth, 6 fine near base). Pronotum with variable-length setae around entire margin, angles rounded. Mesonotum margined laterally and anteriorly with stiff setae. Abdomen concolorous; dorsum covered with fine setae; setation less dense ventrally; membranes with chloride cells. Cercal segments with 1 long dorsal and 1 ventral seta posteriorly; setal length subequal to segment length.

EGG.—Length 500 µm; width 250 µm. General shape oval; cross section circular. Color light golden brown. Collar and eclosion line absent; chorion covered with irregularly hexagonal follicle cell impressions, with walls of varying thickness and occasionally broken; follicle cell impression floors with 2–6 central raised areas (Fig. 13).

DISTRIBUTION.—This species is known only from lower elevations in the Sierra Nevada of California.

TYPES.—Holotype male, allotype female, and 5 male and 10 female paratypes collected from California, Nevada County, Sweetland Creek, Hwy 49, 3.2 km south of North San Juan, 18 May 1983, R.W. Baumann, R.C. Mower, and M.F. Whiting. Holotype and allotype deposited in the U.S. National Museum, Washington, D.C. Paratypes were examined from the following localities: Amador Co.: Big Indian Creek, 6 km north of Plymouth, 11-IV-1986, R.L. Bottorff, 1 female; 25-IV-1986, 1 male, 1 female; 29-IV-1986, 1 female; 9-V-1986, 1 male; Little Indian Creek, 3 km west of Plymouth, 18-IV-1986, R.L. Bottorff, 3 males, 5 females, 1 nymph; 9-V-1986, 2 females; 1-V-1987, 1 female; 12-V-1987, 2 males, 3 females. El Dorado Co.: Indian Creek, 3.3 km northeast of Michigan Bar bridge, 8-IV-1987, R.L. Bottorff, 15 males, 10 females, 1 nymph; 13-IV-1987, 5 males, 2 females; unnamed north bank tributary to Cosumnes River, 2.9 km upstream of Michigan Bar bridge, 9-IV-1986, R.L. Bottorff, 16 males, 13 females, 14 nymphs; unnamed creek tributary to north bank of North Cosumnes River, 6 km north of Nashville, I-V-1987, R.L. Bottorff, 1 male, 3 females, 1 nymph; 12-V-1987, 15 males, 19 females, 25 nymphs. Mariposa Co.: Maxwell River near Coulterville, 25-V-1974, D.G. Denning, 2 females (USNM). Sacramento Co.: Cosumnes River at Michigan Bar, 6-IV-1983, R.L. Bottorff, 1 female; unnamed south bank tributary to Cosumnes River, 0.3 km upstream of the Michigan Bar bridge, 21-III-1986, R.L. Bottorff, 25 males, 16 females, 2 nymphs; 29-III-1986, 17 males, 21 females, 3 nymphs; 11-IV-1986, 25 males, 20 females, 5 nymphs; 29-IV-1986, 24 males, 23 females; 25-III-1987, 14 nymphs. Paratypes are in the collections of the M.L. Bean Life Science Museum, Brigham Young University, Provo, Utah, and R.L. Bottorff, South Lake Tahoe, California.

ETYMOLOGY.—This species is named for the Sierra Nevada of California.

BIOLOGICAL NOTES.—*Suwallia sierra* emerged from late March to mid-May and occurred in low-elevation, small, often intermittent streams with *Bolshecapnia maculata* (Jewett), *Cosumnoperla hypocrena* Szczytko and Bottorff, *Isoperla acula* Jewett, *Isoperla adunca* Jewett, *Isoperla miwok* Bottorff and Szczytko, *Oemopteryx vanduzeea* (Claassen), and *Sweltsa californica* (Jewett). Nymphal gut contents included chironomid larvae, diatoms, and fine organic detritus. Well-developed eggs were found in mature nymphs.

DIAGNOSIS.—Because the epiproct tip is a hairy membraneous knob, the fused basal plate star-shaped, the aedeagus spinulated, and the adult mandibles reduced, *S. sierra* is clearly within the tribe Suwalliini (Surdick 1985), which includes the genera *Suwallia* and *Neaviperla*. Although *S. sierra* shares important characters with *Neaviperla*, such as cerci with modified basal segments and an aedeagus with sclerotized lateral patches, we have assigned this species to *Suwallia* based on the adult meso- and metanota U-marks and the shape of the male basal plate. The most important feature absent in *S. sierra* males that characterizes *Suwallia* is the lack of distinct, medially directed, digitate processes on the hemiterga. In *S. sierra* the hemiterga have medially directed points, but these are not attenuated into the typical digitate processes of *Suwallia* and are smaller than the digitate processes of *Neaviperla*. *Suwallia sierra* is not placed in *Neaviperla* because of important character differences, including the lack of an anteriorly projecting process on the 9th tergum of the male, lack of a bifurcated anterior edge on the male basal plate, less modified basal segments of the male cerci, dark U-shaped pattern on the adult meso- and metanota, and lack of an egg collar. Apparently, *S. sierra* is intermediate in appearance between *Suwallia* and *Neaviperla forcipata* (Neave).

Suwallia sierra males differ from all other *Suwallia* by (1) the greatly reduced hemitergal processes; (2) elongated and curved basal cercal segments, which possess stout spines on the interior surface; (3) excavated, instead of posteriorly produced, 9th tergum; and (4) lateral sclerotized patches on the aedeagus. Female *Suwallia* often cannot be clearly identified to species, although *S. sierra* females do differ slightly by having a more swollen posterior lobe on the subgenital plate, and this lobe projects posteriorly rather than ventrally. *Suwallia* nymphs cannot be separated at this time. The eggs of *S. sierra* are distinctive by lacking a collar and having hexagonal reticulations (Fig. 13).

Suwallia sierra was found in the same major drainage basin of the central Sierra Nevada with 2 other *Suwallia* species; however, it is separated spatially and temporally from both species: *S. pallidula* occurs in middle-elevation perennial streams and emerges in June–August, and *S. autumna* occurs in high-elevation perennial streams and emerges in August–September.

Sweltsa pisteri, new species

Figs. 6–8

MALE.—Macropterous. Body length 7–8 mm; forewing length 8–9 mm. General body color yellow-brown. Dorsum of head, from hind ocelli to front margin, brown. Pronotum with dark margin and dark lateral rugosities, with lateral disks light and corners rounded. Meso- and metanota with dark U-marks. Wings light brown and veins slightly darker. Abdomen with dark brown, median stripe that extends to anterior margin of 8th tergum. Ninth tergum bearing small, rounded, sclerotized knob medially. Tenth tergum with large, V-shaped, darkly sclerotized area located under apex of epiproct; hemiterga sclerotized and bearing long hairs (Fig. 8). Epiproct large and well developed, lightly sclerotized dorsally, tip with round, sclerotized cap that extends ventrally; dorsal aspect nearly parallel sided but sometimes slightly narrower at base or near apex; lateral aspect flat dorsally, thin near base, with massive, rectangular-shaped apex, encompassing apical 2/3, dorsal outline straight (Figs. 6, 7).

FEMALE.—Macropterous. Body length 8.5 mm; forewing length 9 mm. General body color similar to male. Subgenital plate with broad base, narrowly constricted posteriorly, forming pointed tip. The apex is gently rounded but is much narrower than in most *Sweltsa* species.

DISTRIBUTION.—*Sweltsa pisteri* is presently known from the Coast Range in northern California.

TYPES.—Holotype male and allotype female collected from California, Mendocino County, South Caspar Creek, Jackson State Forest, east of Caspar, 9 May 1991, R.L. Bottorff. The holotype male and allotype female are deposited at the U.S. National Museum, Washington, D.C. Paratypes were studied from the following places: Marin Co., Woodacre, 1-V-1955, S.W. Hitchcock, 1 male (USNM); Lily Pond, Alpine Lake (malaise trap), 10-V–9-VI-1970, 6 males, 6 females (CNC). Mendocino Co., same data as holotype, 18-IV-1985, 1 male.

ETYMOLOGY.—This species is named for Edwin P. Pister of Bishop, California. Phil has long been a supporter of rare species and endangered habitats. *Sweltsa pisteri* is presently in this category and needs to be better understood.

DIAGNOSIS.—The male genitalia of *S. pisteri* are most similar to *Sweltsa tamalpa* Ricker, *Sweltsa townesi* Ricker (Figs. 9, 10), and *Sweltsa resima* Surdick (Figs. 11, 12). Both *S. pisteri* and *S. tamalpa* bear a sclerotized prong on their 9th tergum, but it is small and delicate in *S. pisteri* (Fig. 8), while it is large and bears broadly sclerotized lateral bands in *S. tamalpa* (Ricker 1952, Fig. 140). The lateral outline of the epiproct has a downward-pointed projection in *S. tamalpa*, but in *S. pisteri*, *S. resima*, and *S. townesi* it is broad and flat. In dorsal view the epiproct is pointed in *S. tamalpa*, enlarged apically in *S. resima* and *S. townesi*, and nearly parallel in *S. pisteri*. The female subgenital plate of *S. pisteri* is narrow at the tip as in *S. tamalpa* (Ricker 1952, Fig. 143) but not bifurcate or as sharply pointed.

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HOMING IN EASTERN FENCE LIZARDS (*SCELOPORUS UNDULATUS*) FOLLOWING SHORT-DISTANCE TRANSLOCATION

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ABSTRACT.—We conducted an experiment on eastern fence lizards (*Sceloporus undulatus*) during August–September 1995 near Los Alamos, New Mexico, (1) to ascertain if lizards that were relocated short distances exhibited homing, (2) to investigate a possible barrier to movement, and (3) to determine the effect of translocating individuals from a transplant area on lizards in a recipient area. We relocated 15 of an estimated population of 39 (95% CI 36–45) lizards an average distance of 46 m. Fourteen of 15 translocated lizards returned to within 6.81 ($s_{\overline{x}}$ = 1.43) m of the original capture location. Movement distances did not vary (F = 0.76; 1,53 df; P = 0.381) between resident and translocated lizards during the pretreatment period and did not vary for resident (F = 2.86; 1,12 df; P = 0.1166), but varied between pretreatment and posttreatment periods for translocated (F = 14.65, 1,7 df, P = 0.0065) lizards. Translocated lizards did not affect the resighting probability of resident lizards (F = 0.96; 1,14 df; P = 0.34), but this may be related to low power ($1 - \beta$ = 0.15) and translocated lizards moving out of the area quickly.

Key words: barrier, disturbance, eastern fence lizard, Sceloporus undulatus, *homing, New Mexico, translocation.*

Some reptile species may be relocated to mitigate habitat-related conflicts or for humane reasons (Dodd and Seigel 1991); nevertheless, *Sceloporus* spp. may exhibit homing (Noble 1934, Mayhew 1963, Weintraub 1970, Guyer 1978, Ellis-Quinn and Simon 1989), thus reducing the effectiveness of translocations. If eastern fence lizards (*Sceloporus undulatus*) are translocated, it is unknown whether a subsequent increase in density in surrounding areas may cause some individuals in the resident population to be adversely affected (e.g., see Noble 1934, Tubbs 1975, Reinert 1991, Gordon 1994).

Thick vegetation or open habitat may form barriers to dispersal and movements for eastern fence lizards (Noble 1934, Jones and Droge 1980, Tinkle 1982). The ability of animals to traverse the surrounding habitat matrix may determine the number of animals reaching a given distance from or returning to a source population; however, corridors may provide important landscape components for dispersing animals (Noss 1983, Inglis and Underwood 1992).

This study was designed to determine if lizards translocated <70 m across a 55 × 17-m-wide patch of vegetation would return to the site of capture or remain in a different locale. Additionally, we simulated an immigration event and investigated the effect of transplants on resident lizards in a different area.

The study was conducted on a 4355-m^2 area located in Los Alamos, New Mexico (35°53′ N, 106°20′ W), at an elevation of 2165 m. The study site is divided into a south (1520 m^2) and north (1900 m^2) area by a 55 × 17-m patch of dense vegetation, which is bordered on the southern portion of the north side by a 3-m-wide arroyo. Each area is composed of moderate to steep tallus slopes with a wide range of boulder sizes; a nearly vertical canyon wall creates a boundary for approximately one-half of these areas. The site also contains a 0.5-m-wide trail, running approximately south–north, which connects the 2 areas and may provide a corridor for movements. Predominant vegetation in the 55 × 17-m-wide interstitial area consists of brome (*Bromus* spp.), yarrow (*Achilla lanulosa*), apache plume (*Fallugia paradoxa*), and ponderosa pine (*Pinus ponderosa*).

We captured, marked, and/or resighted eastern fence lizards during daily surveys that lasted approximately 1.5 h during the mornings of 14–17, 20–25, and 28 August 1995. Lizards were sexed, measured from snout to vent (SVL), and individually marked using canary yellow Liquid Paper® (The Gillette Co., Boston, MA) with a 1 × 1.5-cm number on their dorsal

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surface. We assumed marking did not affect lizards (Noble 1934, Jones and Ferguson 1980).

Prior to initiating the experiment, we conducted mark-resight surveys and estimated a daily population size of 39 (95% CI = 36–45; Hein and Myers 1995). Minimum daily movement distances were determined during mark-resight surveys conducted in the pretreatment period (i.e., 14–28 August) by measuring the distance from the first sighting of an individual to the next sighting on subsequent days. Resighting probabilities (c) were calculated by summing the number of times each resident lizard was observed, divided by the number of surveys past the initial capture and marking, during pretreatment (c_{pre}) and posttreatment (c_{post}) periods. We translocated lizards during 29–31 August 1995 and continued resighting lizards through 3 September 1995. We also surveyed the study area on 19 September 1995 for 1 h.

We randomly selected the south area as the transplant population, meaning recaptured individuals were relocated to the north area. We attempted to recapture all lizards (transplants and residents) and remark with Liquid Paper®. Resident lizards were released at the site of recapture. The north area was subdivided into a grid of 4 equal-area cells, with each cell approximately 475 m^2. We randomly selected 1 of the 4 cells to receive the first translocated lizard; subsequent lizards were systematically placed in the next higher numbered cell. Translocated lizards were placed in the center of each cell. The shortest distance that lizards were relocated was greater than the largest radii calculated from reported home range estimates (13.0 m, Turner et al. 1969; 15.0 m, Martins 1994); therefore, translocated lizards were believed to have been displaced outside the normal range of their movements. Unmarked lizards captured on the south side were also marked and translocated. We measured the straight-line distance from each capture location (south) to each release site (north) and the distance from each subsequent resighting to the original point of capture until the lizard was within 10 m of the capture location or the study ended. Straight-line distances were used to calculate Griffin's index (Griffin 1952, Weintraub 1970), which measures the directness of a translocated animal's return (i.e., homing) path. Successful homing, following translocation, was defined as moving from the north to the south side of the canyon to within the area where we had repeatedly observed each individual, or within 10 m of the original point of capture for individuals that were not observed prior to translocating. We also measured long-distance movements for 2 lizards (ID nos. 2 and 18) that were observed twice during 1 survey.

All distances were normalized by log transformation prior to analyses. We compared mean distances moved and SVL between transplant and resident lizards during the pretreatment period using analysis of variance, whereas SVL in relation to distances moved was compared using regression (PROC GLM, SAS Institute Inc. 1988). All other comparisons of distances that individual lizards moved were tested using a repeated measure analysis of variance (PROC GLM, SAS Institute Inc. 1988). We also tested whether transplants adversely affected residents by comparing resighting probabilities among resident lizards between pretreatment and posttreatment periods using a repeated measure analysis of variance (PROC GLM, SAS Institute Inc. 1988). Because we used a repeated measures analysis of variance, each lizard acted as its own control, and the normal between experimental unit (i.e., lizard-to-lizard) variation from the error sum of squares was thus removed. Power ($1 - \beta$) of tests was also calculated for each comparison (SAS Institute Inc. 1988).

RESULTS

Movement distances did not vary ($F = 0.76$; 1,53 df; $P = 0.381$; $1 - \beta = 0.83$) between the resident and transplanted lizards during the pretreatment period and did not vary between periods for resident ($F = 2.86$; 1,12 df; $P = 0.1166$; $1 - \beta = 0.34$) lizards, but they varied between periods for translocated ($F = 14.65$; 1,7 df; $P = 0.0065$; $1 - \beta = 0.91$) lizards. Additionally, distances moved by lizards between north and south areas differed between pretreatment and posttreatment periods ($F = 15.80$; 1,19 df; $P = 0.0008$; $1 - \beta = 1.00$). SVL did not differ ($F = 1.89$; 1,115 df; $P = 0.171$; $1 - \beta = 0.28$) between transplant and resident lizards. There was no relationship between SVL and distance moved ($F = 1.65$; 16,34 df; $P = 0.107$; $1 - \beta = 0.79$) between lizards during the pretreatment period.

Thirteen of 15 (7 female, 8 male) translocated lizards exhibited homing by moving to the

TABLE 1. Summary of eastern fence lizards translocated <75 m in Los Alamos, New Mexico, during August–September 1995.

ID	Sex	SVL (mm)	Translocated distance (m)	Homed distance[a] (m)	No. days to home	Griffin's index
1	F	77	41.20	4.02	3	1.05
2	M	60	65.80	15.40	1	1.40
4	F	56	23.80	16.29	2	1.04
7	F	67	38.80	9.40	1	1.04
10	F	66	51.05	2.89	3	1.07
11	M	46	59.70	5.00	≤21	1.02
15	M	56	57.50	3.20	1	1.12
18	M	60	63.40	1.85	1	1.39
42	F	66	40.40	—[b]	—	—
43	M	57	49.35	8.80	2	1.17
44	F	62	40.70	7.26	2	1.20
45	M	48	39.05	11.65	3	1.95
46	M	66	37.50	1.69	3	1.09
47	M	52	59.03	1.10	3	1.02
48	F	57	31.20	5.09	1	1.64

[a] Distance from the original point of capture prior to translocating.

[b] Did not demonstrate homing, but was resighted 1 time in the northern area.

south side of the canyon, within an average of 6.81 ($s_{\bar{x}}$ = 1.43) m of the original capture point in 2 d ($s_{\bar{x}}$ = 0.25; Table 1). Translocated lizards moved an average of 7.68 ($s_{\bar{x}}$ = 1.47) and 22.17 m ($s_{\bar{x}}$ = 4.42), whereas resident lizards moved an average of 6.37 ($s_{\bar{x}}$ = 1.0) and 10.0 m ($s_{\bar{x}}$ = 1.68) during pretreatment and posttreatment periods, respectively. One additional translocated lizard was observed within 5 m of the original point of capture on 19 September 1995. Griffin's index averaged 1.20 ($s_{\bar{x}}$ = 0.07), indicating that, on average, translocated lizards moved 1.2 times the relocated distance as they were returning to the capture location. Lizards 2 and 18 moved 43.1 and 16.4 m in 71 and 80 min, respectively.

Eight (4 female, 4 male) of 14 lizards were recaptured and translocated, whereas 7 (3 female, 4 male) unmarked lizards were captured and relocated. We recaptured and remarked 10 (2 female, 8 male) of 18 resident lizards and did not capture or sight any unmarked lizards in the resident area. Fifteen of 18 resident lizards were resighted an average of 2.17 ($s_{\bar{x}}$ = 0.29) times during the experiment. During the study, lizards were captured and/or resighted on the canyon floor, tallus slopes, and corridors (i.e., trail and stream), whereas no marked lizards were captured or resighted and no unmarked lizards were observed in the patch of vegetation.

Resighting probabilities did not differ (F = 0.96; 1,14 df; P = 0.34) between pretreatment (c_{pre} = 0.58, $s_{\bar{x}}$ = 0.06) and posttreatment (c_{post} = 0.49, $s_{\bar{x}}$ = 0.05) periods for individual resident lizards, but this may be related to low statistical power ($1 - \beta = 0.15$) because of a small effect size (0.09) and/or sample size (n = 15).

DISCUSSION

In our study the majority (14 of 15) of eastern fence lizards exhibited homing by returning to the south side of the canyon, with most (11 of 14) lizards returning to <10 m from the original capture location. This finding agrees with other studies that demonstrated homing in lizards (*Sceloporus* spp.) that were translocated ≤ 240 m (Noble 1934), ≤ 150 m (Mayhew 1963), ≤ 215 m (Weintraub 1970), ≤ 280 m (Guyer 1978), and ≤ 200 m (Ellis-Quinn and Simon 1989). Male and female eastern fence lizards homed equally well (Table 1). Although we did not estimate home ranges, the minimum daily movement distances during the pretreatment period indicate that all lizards were relatively sedentary; however, we cannot rule out that some translocated individuals may have been familiar with the northern area, and we suspect that lizards successfully homed because translocated distances were relatively short (i.e., ≤ 65.8 m). No lizards were observed in the patch of dense vegetation; it may have inhibited movements. Alternatively, lizards were observed on or near the small trail and streambed, which suggests these features may have been used as corridors between the 2 areas; corridors may provide important landscape components for dispersing animals (Noss 1983, Inglis and Underwood 1992).

We did not detect an effect on the resighting probabilities of resident lizards by translocated lizards, but our test had poor power ($1 - \beta = 0.15$) because of a low effect size (0.09) and small sample size ($n = 15$). If the effect size had been large (e.g., >0.45), which might imply the biological significance of an immigration event was high, then the power of this test would have been strong (i.e., >0.80). We resighted 15 of 18 residents ≥1 time during the experiment, suggesting translocated lizards did not cause resident lizards to emigrate; however, lizards were capable of moving large distances in a short amount of time, and the translocated lizards spent relatively little time (2 d) among the residents. The amount of time for translocated lizards to home was shorter than studies that displaced *Sceloporus* spp. greater distances than our study (Noble 1934, Ellis-Quinn and Simon 1989), but similar to a study with shorter (<125 m) displacement distances (Weintraub 1970).

We did not detect any deleterious effects of translocating lizards on the resident lizards; however, if small-scale habitat disturbance causes fence lizards to emigrate into neighboring areas, resident lizards in these areas may be affected. Translocating eastern fence lizards may cause residents to display aggressively or attack (Noble 1934), which may affect survival and reproduction (Vinegar 1975). Similarly, artificial crowding may affect *Sceloporus* spp. by reducing growth and/or survival rates (Tubbs 1975). Consequently, future studies should investigate whether translocated or resident lizards are affected (e.g., increased aggression or lower survival) by immigration events.

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NEW VARIETY OF *ASTRAGALUS CONJUNCTUS* S. WATSON FROM BENTON COUNTY, WASHINGTON

Stanley L. Welsh[1], Florence Caplow[2], and Kathryn Beck[2]

ABSTRACT.—Discussed are relationships of the species within *Astragalus* section Conjuncti; *A. conjunctus* var. *rickardii* Welsh, Beck, & Caplow var. nov. is proposed.

Key words: Astragalus conjunctus, *Conjuncti, Washington.*

In 1984 a collection of plants from the Hanford Atomic Energy Plant, taken by Gary Baird, arrived at the herbarium at BRY. Among the specimens were several collections of an *Astragalus* obviously belonging to the section Conjuncti as proposed by Barneby (1964). The section is characterized by having stipules connate at the lowermost nodes and greatly shortened lower internodes with the upper one or few elongating, the leaves thus disposed in a subbasal tuft (Barneby 1964, Isely 1996). Commonly, most of the plant height is attributable to elongated peduncles and racemes. The Hanford specimens have erect, sessile pods similar to those of all other members of the Conjuncti except for *A. leibergii,* in which the pods are stipitate.

However, the plants from Hanford have strigulose pods, merely strigose vesture otherwise, banner reflexed through about 45°, and rather short-cylindric calyces. Thus, they do not fit exactly within any of the species outlined in the Atlas of North American Species of *Astragalus* (Barneby 1964). Dr. Barneby graciously examined the plants and indicated their close relationship with *A. conjunctus* S. Watson. The present writers concur, though the collections by Baird from 1984 and more recent collections taken by Kathryn Beck and Florence Caplow in 1995 represent a slight northward extension of that species into Washington. Both the Baird and Beck and Caplow materials represent relatively uniform plants taken in 2 main localities in Benton County, Washington, one southwest of Kiona and the other north-northwest of Benton City, on Rattlesnake Ridge in the Hanford Reservation, U.S. Department of Energy (Fig. 1).

Rattlesnake Ridge is within an area established as the Fitzner-Eberhardt Arid Lands Ecology Reserve, a high-quality native shrub-steppe environment.

The Benton County plants were subsequently compared with materials obtained on loan from Oregon State University (OSC, including WILU) through the kindness of Dr. Aaron Liston. The OSC and WILU collections include specimens of all species of section Conjuncti and demonstrate the considerable range of variation within the individual species. Main variation within the species complex involves flower size, pod length/width ratio, and degree of elongation of the upper internodes. The stipe of *A. leibergii* easily distinguishes it from all other taxa within the Conjuncti, and from such look-alikes as *A. sheldonii* (Rydberg) Barneby and *A. reventus* A. Gray, both of which occur adjacent to the range of the Conjuncti phalanx. These latter, both relegated to section Reventi-arrecti (subsection Reventi-arrecti), have similar overall habit, but lowermost stipules are distinct.

A single specimen from OSC (Lawrence 99, 26 June 1917) is similar to the Benton County materials. It is from Wasco County, Oregon, 12 miles southeast of The Dalles, near Rice Station, in a bunchgrass prairie and transition scabland, with the notation "protected from grazing this season." It is in fruit only. The pods are strigulose as in the Benton County plants and bear the notations *A. reventus* and *A. hoodianus*. The specimen's features are mainly those of *A.*

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conjunctus sens. lat., and the collection is tentatively identified as belonging to the Benton County plants here regarded as var. *rickardii*. Certainly the collection site should be revisited.

A key to the species of Conjuncti, differing considerably from that published by Barneby (1964), is presented below. Following the species key is a description of *A. conjunctus* and a key to the closely related taxa as herein interpreted.

Section Conjuncti

1. Pods (and ovaries) stipitate, the stipe at least 3 mm long; plants of Kittitas, Chelan, and Douglas counties, Washington. . . . . *A. leibergii* M.E. Jones

1. Pods (and ovaries) sessile; plants of various distribution in Oregon, Washington, and adjacent Idaho
    2. Pods evidently villous (sometimes glabrous in age); calyx (10) 11–15 mm long, the teeth (2.6) 4.6–6.7 (7.5) mm long; plants within and near the Columbia Gap, Wasco and Hood River counties, Oregon, and Klickitat Co., Washington. . . . . *A. hoodianus* Howell
    2. Pods glabrous or strigulose; calyx and teeth of various length; plants variously distributed
        3. Banner recurved through ca 45°, oblanceolate or broadly rhombic-oblanceolate, emarginate, 16–25.5 mm long, 6.7–10 mm wide; calyx teeth 1.3–3 (4) mm long; pods 5–8 mm thick; plants of Benton Co., Washington, and transmontane Oregon, mostly above 610 m where its range approaches the following: from Wasco to Baker Co., Oregon, southeast into southwest Idaho. . . . *A. conjunctus* S. Watson
        3. Banner strongly recurved through 90°, oblong-oblanceolate, rhombic-oblanceolate, -elliptic, oblong-ovate, or somewhat quadrately ovate-cuneate, usually deeply notched, (13.2) 14–20.7 mm long, 5–9.8 mm wide; calyx teeth (2.4) 2.7–5.1 mm long; pods (4.5) 6–11 mm thick; plants of Klickitat, Yakima, and Kittitas counties, crossing to the south bank of the Columbia in Sherman Co., Oregon . . . . *A. reventiformis* (Rydberg) Barneby

Astragalus conjunctus **S. Watson**, Proc. Amer. Acad. Arts 17: 371. 1882. Basalt milkvetch.

Moderate, subacaulescent or shortly caulescent perennial, 15–65 cm tall, from a superficial branching caudex. **Pubescence** strigulose, basifixed. **Stems** erect or ascending, several to numerous in bushy clumps. **Stipules** 3–10 (11) mm long, at least the lowermost connate-sheathing. **Leaves** (6) 10–30 cm long, mostly in a subbasal cluster; leaflets (9) 13–25 (31), 3–23 mm long, linear-oblong, -elliptic, lanceolate or subfiliform, obtuse, acute, or retuse, the terminal one continuous with the rachis, pubescent below and above. **Peduncles** 10–33 cm long; racemes 7- to 17 (20)-flowered, the flowers ascending to spreading at anthesis, the axis (3) 4–12 (15) cm long in fruit; bracts 2–4.5 mm long; pedicels 1–4.5 mm long; bracteoles 2; calyx (7) 8.5–12 mm long, the tube (5.7) 6–9.2 mm long, 2.5–4 mm wide, cylindric or subcylindric, strigulose-pilosulous, the teeth 1.3–3 (4) mm long, subulate. **Flowers** 16–25.5 mm long, whitish with keel tip and other petals tipped with purple, the banner recurved through ca 45°. **Pods** erect, sessile, oblong-ellipsoid to narrowly oblong-ovoid, straight or slightly incurved, 12–25 mm long, 5–8 mm thick, obcompressed, glabrous or strigulose, subbilocular, the septum to 1.4 mm wide; ovules 23–30.

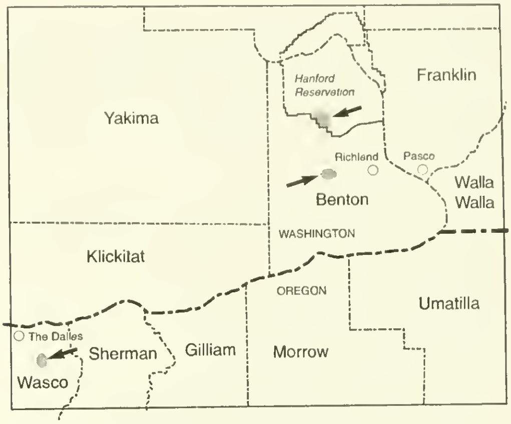

Fig. 1. Portions of Washington and Oregon, showing locations of *Astragalus conjunctus* var. *rickardii* Welsh, Beck & Caplow.

1. Calyx tube cylindric to subcylindric, 4.9–9.2 mm long; pods glabrous, 5–8 mm thick; plants widespread . . . . var. *conjunctus*
1. Calyx tube campanulate to subcylindric, 4.9–6.2 mm long; pods strigulose, 4.3–5 mm thick; plants local in Benton Co., Washington, and Wasco Co., Oregon . . . . var. *rickardii*

Astragalus conjunctus var. *conjunctus*

[*A. reventus* var. *conjunctus* (S. Watson) M.E. Jones; *Phaca conjuncta* (S. Watson) Piper; *Tium conjunctum* (Watson) Rydberg].

Peduncles 10–33 cm long; racemes 7- to 17 (20)-flowered, the axis (3) 4–12 (15) cm long in fruit; pedicels 1–4.5 mm long; calyx (7) 8.5–12 mm long, the tube (5.7) 6–9.2 mm long, cylindric or subcylindric, the teeth 1.3–3 (4) mm long. **Flowers** 16–25.5 mm long. **Pods** 12–25 mm long, 5–8 mm thick, glabrous; ovules 23–30. Type: "In John Day Valley, Oregon (J. Howell, in May, 1880) and on sterile rocky ridges in Baker County, by W. C. Cusick, 1881"; holotype GH!; isotypes ORE, WS; paratypes GH!, ORE.

Meadows, brushy slopes, grasslands, sagebrush desert, and pine forests, on basaltic bedrock, at 485 to 1555 m, from the Blue Mountains, Baker Co., west to the Deschutes River, and south to the Malheur Valley, Steens Mountain, Oregon, and east to Owyhee Co., Idaho.

Astragalus conjunctus var. *rickardii* Welsh, Beck, & Caplow, var. nov.

Similis *A. conjuncti* var. *conjuncti* in habitu, sed in leguminibus pubescentibus et angustioribus, et floribus minoribus generaliter differt.

Peduncles 5–26 cm long; racemes 10- to 19-flowered, the axis 4–13 cm long in fruit; pedicels 1–2.5 mm long; calyx 7–9 mm long, the tube 4.9–6.2 mm long, campanulate, the teeth 1.5–3 mm long. **Flowers** (13.2) 14–20.7 mm long. **Pods** 13–20 mm long, 4.3–5 mm thick, strigulose; ovules 15–20.

TYPE.—Washington, Benton Co.; T11N, R26E, S30, NW/SW, on northeast-facing slopes of Rattlesnake Mountain, with sagebrush and Sandberg bluegrass, at ca 1036 m, 29 May 1995, Kathryn Beck & Florence Caplow 95083, holotype BRY!, isotypes NY!, US!, WTU!, WS!

ADDITIONAL SPECIMENS (PARATYPES).—Washington, Benton Co.: Rattlesnake Hills, ca 1 mi NW of Bennett Ranch, 18 May 1984, G. Baird 794; north slope of Horse Heaven Hills, along McBee Rd, 12 May 1984, G. Baird 734; Rattlesnake Hills, above Snively Basin, 18 May 1984, G. Baird 775; Horse Heaven Hills, near Chandler Butte, 14 April 1995, K. Beck & F. Caplow 95022; Rattlesnake Mountain, 14 May 1995, K. Beck & F. Caplow 95038; Horse Heaven Hills, near Chandler Butte, 22 May 1995, K. Beck & F. Caplow 95064 (all BRY!). Washington, Wasco Co. (see Lawrence 99, cited above).

Bunchgrass-sagebrush community at 450 to 1070 m, on the Hanford Atomic Energy Site, Benton Co., Washington, and bunchgrass-scabland community, Wasco Co., Washington.

Relationships within the Conjuncti are problematical, all taxa being closely alike. The taxon proposed here appears to share features of both *A. conjunctus* and *A. reventiformis*. The calyx tube proportions are similar to those of the only slightly disjunct *A. reventiformis*, but the calyx measurements are smaller than for that taxon. Furthermore, proportions of the calyx tube length-width ratio within *A. conjunctus* in a strict sense differ only in degree from those of var. *rickardii*. The presence of pubescence in pods within the genus rises and falls but is apparently uniform in the Benton County plants. Pod pubescence is herein considered diagnostic and seems to be correlated with relatively shorter calyces and narrower pods. Some specimens assigned to *A. reventiformis* from nearby Yakima County (Caplow & Beck 95075, 96003, and Baird 633) have pods absolutely and proportionately as narrow as those of the proposed new variety. The pods in those specimens are, however, glabrous.

The taxon is named in honor of Dr. Bill Rickard, one of those responsible for establishment of the Fitzner-Eberhardt Arid Lands Ecological Reserve.

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COYOTE ACTIVITY PATTERNS IN THE SIERRA NEVADA

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Key words: activity patterns, California, Canis latrans, *coyote, Sierra Nevada.*

The winter months in high mountain regions of the Sierra Nevada make survival difficult for predators that exist there. High productivity during the spring and summer enables coyotes (*Canis latrans*) to survive and reproduce, but little is known about how these animals overwinter in mountainous areas. Hawthorne (1970) suggested that coyotes make altitudinal migrations, but recent data (Gantz 1990, Gese et al. 1996, Shivik et al. 1996) indicate that coyotes can remain in the high mountains throughout the year.

Temporal rhythms (e.g., innate behavioral rhythms such as diel cycles and seasonal reproductive cycles) may influence, or help elucidate, coyote activity patterns. We hypothesized that coyotes vary activity levels throughout the year as a result of these seasonal biological requirements. We related coyote activity patterns to the seasons that are likely to influence these patterns. We analyzed coyote activity in the Sagehen Basin of the Sierra Nevada because seasonal activity patterns in this seasonally cold and snowy climate provide insight into how coyotes allocate energy in order to survive and reproduce.

Previous analyses of coyote activity used movement data to determine activity levels (Gipson and Sealander 1972, Andelt and Gipson 1979, Smith et al. 1981, Gese et al. 1989). However, some authors argued that using distance traveled is not a good measure of coyote activity (Knowlton et al. 1968, Laundré and Keller 1981). The literature presents a paucity of analyses examining seasonal trends in coyote activity using activity-sensitive collars (especially in mountainous areas). Therefore, we conducted a study using activity-sensitive radiocollars to monitor seasonal coyote activity in a mountainous region of the Sierra Nevada.

MATERIALS AND METHODS

We conducted our research in the 105-km^2 watershed surrounding the University of California Sagehen Research Station, approximately 13 km north of Truckee, California, in the Tahoe National Forest. Elevation ranges from 1880 to 2620 m. The area is characterized by long, cold winters and warm, dry summers with nightly temperatures falling below 0°C, often at all times of year. Most of the annual precipitation (91 cm) falls as snow during winter. Forested areas are dominated by Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*). Brush fields contain deerbrush (*Ceanothus velutinus*) and greenleaf manzanita (*Arctostaphylos patula*). Sagebrush (*Artemisia tridentata*) dominates on lower, dry slopes. Small stands of lodgepole pine (*Pinus contorta* var. *murryana*) and aspen (*Populus tremuloides*) occur near springs, meadows, and streams. Red fir (*Abies magnifica*), mountain hemlock (*Tsuga mertensiana*), and western white pine (*Pinus monticola*) dominate at higher elevations (Morrison et al. 1985).

We trapped coyotes using steel leghold traps with offset, padded jaws and short anchor chains to minimize trapping injury and stress (Hawthorne 1970, Olsen et al. 1986). Coyotes were immobilized physically (with a pin-stick and then vet-wrap or electrical tape). The sex, weight, age (Gier 1968), and general condition were recorded for each captured coyote (Shivik 1995). During the course of the study, we made 18 captures of 16 coyotes during 3 trapping periods.

Radiocollars with signal-pulse varying activity switches (Model 400; Telonics, 932 E. Impala Ave., Mesa, AZ 85204-6699) were fitted to each coyote. These collars transmitted a 75 pulse/

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min signal when the collar was moving and a 50 pulse/min signal when it was stationary for over 1 min. Hand testing of the collars indicated that the internal switches were quite sensitive and that a very small amount of movement was required to set the collar into "active" mode. Therefore, for purposes of this study, a nonactive coyote was one that had not moved for over 1 min (and was probably sleeping).

Concurrent with attempts to locate each animal, we monitored collared coyotes for activity during eight 4-hr radio-tracking sessions per week (Shivik et al. 1996). Coyotes were monitored once per hour in 4-hr blocks that bracketed sunrise, middle of the day, sunset, and middle of the night. Each coyote was monitored for approximately 2 min each hour during the 4-hr tracking session. For analysis, data were divided into the following 6-hr categories: "morning" (>0400 and ≤ 1000), "day" (>1000 and ≤ 1600), "evening" (>1600 and ≤ 2200) and "night"(>2200 and ≤ 0400). A coyote's percent activity during each block was the basic dependent variable. We calculated the estimate of percent activity by dividing the number of times the animal was recorded as active by the total number of times it was heard during the block of monitoring if the number of samples was ≥ 2.

The influence of seasonal factors, such as weather patterns, cannot be easily separated from changes due to internally controlled behavioral rhythms. However, to survive and reproduce, coyotes must pursue certain behaviors (e.g., forming pair bonds, maintaining territories, and feeding pups) regardless of environmental conditions. Therefore, we used the biological season as the basis for examining coyote activity through time (Laundré and Keller 1981, Smith et al. 1981). Data were divided into the following seasons for analysis: breeding (1 January–15 March), pre-pup (16 March–30 April), pup rearing (1 May–31 July), and dispersal (1 August–31 December). Data were collected 1 August 1993–31 July 1994.

We assessed activity levels by animal within seasons during the regularly scheduled morning, evening, midday, and midnight tracking sessions, and arcsine transformed the activity rate for each coyote before analysis (Zar 1984). Because seasonal activity could be influenced by the sex of the coyote, we analyzed data using a 2-way ANOVA. We hypothesized differences in activity between sex and season and also used ANOVA to determine whether differences in activity were apparent at different times of day during the biological seasons.

For all analyses, the sample unit was the individual coyote. For example, in the ANOVA of the percent activity by season and day category, all activities of coyote F040 during each season and day category were reduced to a single average to avoid pseudoreplication (Hurlbert 1984). If a significant difference in mean activity level was detected, we performed multiple comparisons using Tukey tests. Statistical assumptions were assessed using residual plots (Kirby 1993).

RESULTS AND DISCUSSION

For the 12 coyotes (7 males and 5 females) monitored, 1368 activity rates were calculated for the 4 time-of-day categories ($\bar{x} = 342$ per season, $\bar{x} = 114$ per coyote) from 2150 observations on individual coyotes ($\bar{x} = 538$ per season). Mean activity varied between seasons ($P < 0.001$), but there was no evidence for a difference in activity by sex ($P = 0.63$) and no interaction between sex and season ($P = 0.192$). Because we did not detect a difference in activity between sexes, we did not partition out the effects of sex in the remaining analyses. Coyote activity during the breeding season was significantly less than the pup ($P < 0.001$) and dispersal ($P = 0.011$) seasons, and activity was less during the pre-pup than the pup ($P = 0.029$) season (Fig. 1). Activity significantly varied by day category only during the dispersal season ($P = 0.033$) when activity peaked during the evening ($\bar{x} = 0.60$, $s_{\bar{x}} = 0.05$) and was lowest during the day ($\bar{x} = 0.42$, $s_{\bar{x}} = 0.04$).

Our results are consistent with those of other researchers who found that coyote activity varied by time of day, even when previous studies used different methods to rate activity and involved different degrees of pseudoreplication (Gipson and Sealander 1972, Andelt and Gipson 1979, Shivik and Crabtree 1995). Furthermore, other studies did not show differences in activity between males and females (Gipson and Sealander 1972, Andelt and Gipson 1979), suggesting that activity rates of males and females do not differ drastically. However, Laundré and Keller (1981) indicated that females travel less than males during the pup season, leading us to hypothesize that,

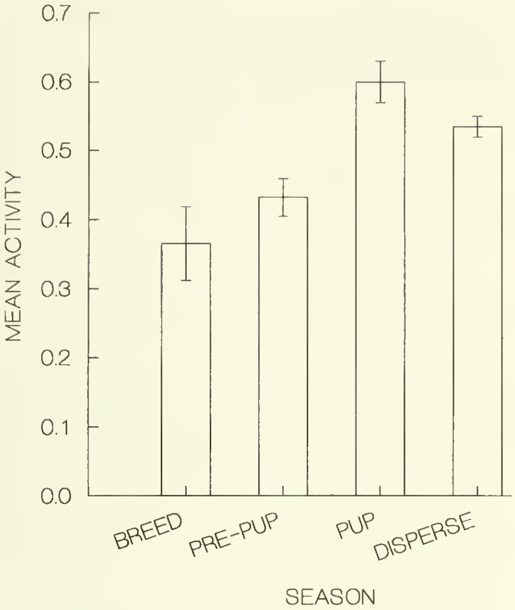

Fig. 1. Seasonal activity of coyotes in the Sagehen Basin of the Sierra Nevada. Bars represent 1 standard error. Means were calculated using each coyote as the sample unit after estimating individual coyote activity within each season. The breeding season was 1 January–15 March (*n* = 7), pre-pup was 16 March–30 April (*n* = 7), pup was 1 May–31 July (n = 11), and dispersal was 1 August–31 December (*n* = 12).

overall, female activity is not reduced but that travel by female coyotes is limited to a smaller area during the pup season. Differences between what the distance traveled metric and absolute activity measure actually represent contribute to confusion regarding seasonal changes in coyote activity (Lanudré and Keller 1984). Female coyotes that are nursing pups would be considered active by our method and not active when using distance-traveled data. A correlation is evident, however, between distance traveled and absolute activity, and therefore both distance traveled and motion-sensitive radiocollar data are useful for examining diel and seasonal coyote activity, noting that each method is sensitive to different behaviors.

Coyotes in Grand Teton National Park rest more during winter months because coyote reliance on carrion reduces the need to hunt small mammal prey (Bekoff and Wells 1980). Similarly, in Yellowstone National Park, coyotes reduce activity as available carcass biomass increases (Gese et al. 1996). During our study coyotes were also less active during winter (breeding and pre-pup seasons), but because deer are absent from this study area in winter, the carcass mechanism for decreased activity proposed by Bekoff and Wells (1980) may not apply to Sagehen coyotes.

The ultimate mechanism for reducing energy expenditures during winter may be that reduced winter activity probably improves chances for individual survival. Because activities such as pup rearing are not occurring, coyotes are able to reduce their levels of activity during winter. This behavioral plasticity allows coyotes to survive and reproduce in mountainous areas, even when carrion (e.g., from winter-kill ungulates) is not available. Thus, the proper currency for examining coyote ability to remain in areas with a seasonally reduced prey base and harsh weather conditions is the amount of time relegated to social and reproductive behaviors. In seasons when activity-intensive behaviors such as pup rearing are not occurring, coyotes reduce energy expenditures and exist in areas with seasonally limited food supplies.

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U.S. DISTRIBUTION OF THE COEUR D'ALENE SALAMANDER (*PLETHODON IDAHOENSIS* SLATER AND SLIPP)

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Key words: Amphibia, salamander, Plethodon, *geographic distribution, Rocky Mountains.*

The Coeur d'Alene salamander (*Plethodon idahoensis*) is the only lungless salamander (Plethodontidae) known from the northern Rocky Mountains. Discovered in 1939 on the Idaho Panhandle (Slater and Slipp 1940), this terrestrial amphibian has since been encountered in northwestern Montana and southeastern British Columbia (Teberg 1964, Holmberg et al. 1984).

Prior to this study, the status and exact locations of some historic *P. idahoensis* collection sites were unknown (Groves 1988). Moreover, the northern Rocky Mountains in the U.S. had not been well surveyed for amphibians (Nussbaum et al. 1983), raising the possibility that additional localities might exist. To assist conservation efforts directed toward this species (Groves 1988), we conducted surveys documenting its occurrence south of Canada. Herein we report results of the study.

We compiled locality data from reviews in Brodie (1970), Brodie and Storm (1970), and Lynch (1984); from unpublished records of Idaho and Montana wildlife agencies; from personal correspondence with individuals having field experience with *P. idahoensis*; and from the collection records of the following museums: California Academy of Sciences, San Francisco (CAS); Museum of Vertebrate Zoology, University of California, Berkeley; American Museum of Natural History, New York; Field Museum of Natural History, Chicago; Museum of Comparative Vertebrate Zoology, Harvard University, Cambridge.

Fieldwork was conducted from 1987 through 1994, primarily during wet weather in spring and fall. Working within and around the geographic range of *P. idahoensis* as it was known previously (Lynch 1984), we surveyed regions accessible by road or trail in Idaho and Montana up to 2000 m elevation and attempted to visit and verify all previously reported localities. We located salamanders by digging, by displacing surface objects, and by night searches with flashlight. Descriptions of localities are listed with the Idaho Natural Heritage Program, Boise, and the Montana Natural Heritage Program, Helena. Voucher specimens have been deposited in CAS, in the Charles R. Conner Museum (CM), Washington State University, Pullman, and in herpetological collections at the University of Idaho (UI).

A locality is here defined as an area of occurrence >0.5 km from another such area. It appears that at least 55 localities were recorded for *P. idahoensis* before the present study. We found vague and incomplete data for some historic collection sites and suspect they may be synonymous with localities for which we have more complete information. The Canadian extent of this species has yet to be completely documented. Three British Columbia localities exist in the Kootenai Valley within 60 km of the U.S.-Canadian border (Orchard 1991).

One hundred thirty-two new localities were discovered during our field surveys. These include the following 3 range extensions: 39 km due NNE of Libby, Lincoln County, Montana, on 9 May 1988 (CM 89-161; 48°44′23″N, 115°19′15″W; 792 m elev.); 6.5 km due W of Victor, Ravalli County, Montana, on 25 May

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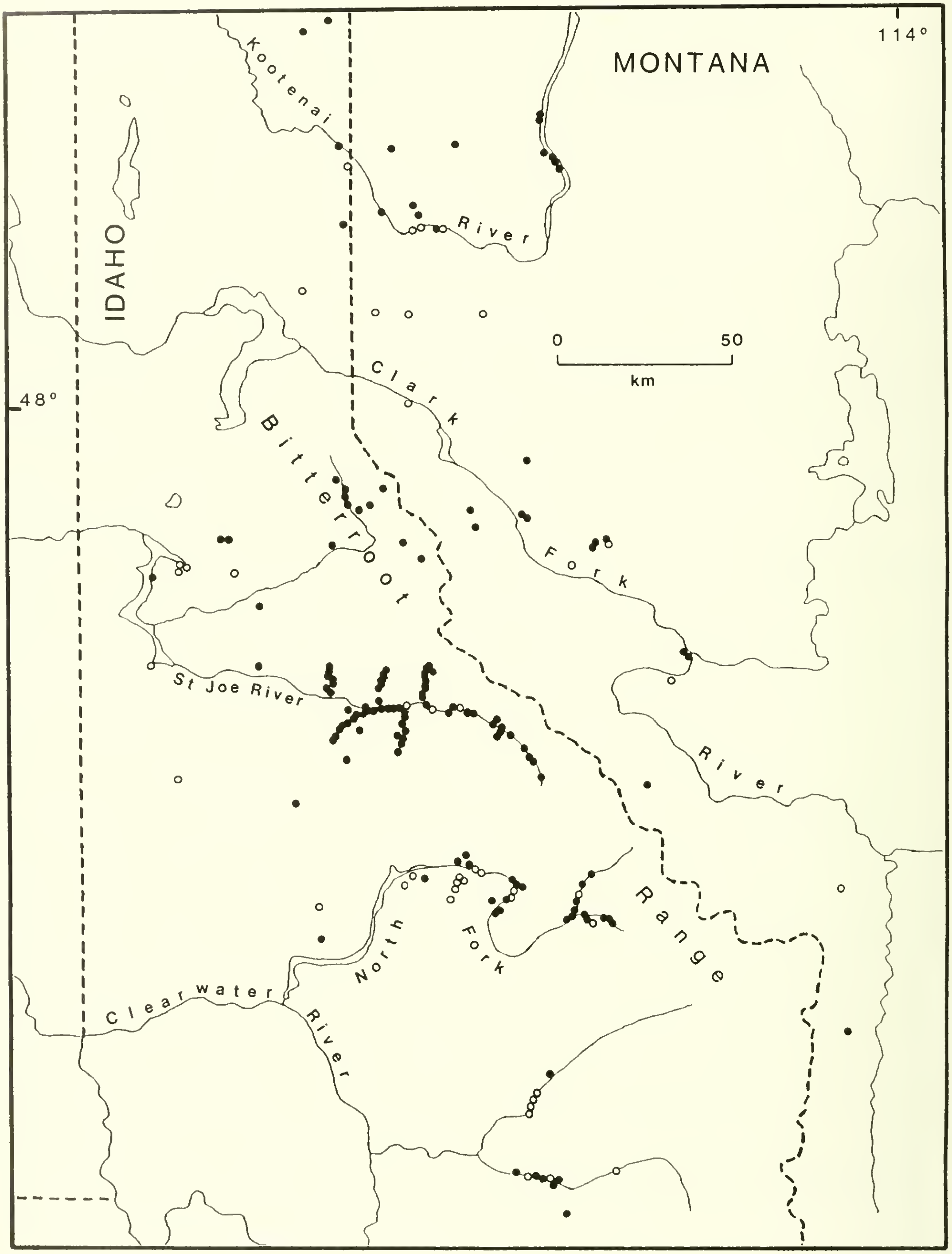
114°
MONTANA
IDAHO
Kootenai
River
48°
0
50
km
Clark
Fork
River
Bitterroot
Range
St Joe River
North
Fork
Clearwater
River

Fig. 1. U.S. distribution of the Coeur d'Alene salamander (*Plethodon idahoensis*). Historic localities are represented by open circles, new localities by closed circles.

1987 (CM 89-163; 46°25′29″N, 114°15′23″W; 1550 m elev.); and 32 km due SE of Lowell, Idaho County, Idaho, on 15 May 1989 (UI IA 627-1; 46°04′35″N, 115°16′16″W; 780 m elev.). In all, these sites extend the species' known range 44 km NE, 87 km E, and 16 km S, respectively (Teberg 1965, Brodie 1970, Lynch 1984).

We found *P. idahoensis* in forested, mountainous regions between 500 and 1550 m elevation. Most localities occur in valleys draining the west slope of the Bitterroot Range of Idaho; the southernmost occur in the Clearwater River drainage (Fig. 1). The species has a scattered distribution in the Clark Fork and Kootenai River drainages of Montana. We commonly encountered the salamander in talus and other rocky debris. Exposures of fractured bedrock are present at almost all localities, and we often observed *P. idahoensis* using fractures as retreats. All localities are affiliated with springs, seepages, or damp areas along streams.

Except for the existence of some marginal lowland populations in xerophytic habitats, distribution of *P. idahoensis* is confined to temperate mesophytic forest types (Daubenmire 1978). The upper altitudinal limits of the salamander coincide with the transition between temperate mesophytic and subalpine communities in the northern Rockies (Arno 1979, Habeck 1987), and exceed those of most western plethodons (Nussbaum et al. 1983).

Plethodon idahoensis is part of a disjunct coastal biota inhabiting the portion of the Rocky Mountains in which maritime climatic influence is strongest (Arno 1979, Johnson 1987, Cooper et al. 1991). Annual precipitation in regions occupied by *P. idahoensis* averages 50–140 cm; the highest levels occur on the west slope of the Bitterroots where the salamander is most abundant (Pacific Northwest River Basins Commission 1969). Through much of its range *P. idahoensis* occupies drier terrain than do other western plethodons at the same latitudes (Dumas 1956, Herrington 1985, Wilson et al. 1995). This species' affinity for stream margins and seepages contributes to its survival in comparatively arid habitats (Wilson and Larsen 1987).

Much precipitation in the northern Rocky Mountains occurs as snow (Finklin 1983), and regions inhabited by *P. idahoensis* have colder, more prolonged winters than those inhabited by most of the salamander's western congeners (Nussbaum et al. 1983). Freezing weather affects distributions of salamanders by limiting time for foraging and reproduction (Lynch 1981). Not surprisingly, *P. idahoensis* occupies drainages with the longest local annual frost-free periods. The Kootenai Valley, which contains the species' northernmost populations, has the longest frost-free season of any forested region in northwestern Montana or southeastern British Columbia (Caprio 1965, Ross and Savage 1967, Farley 1979).

The association of *P. idahoensis* with rocky microhabitat is consistent with reports of other terrestrial salamanders. Talus and rock outcrops favor occurrence of these forms by providing seasonal shelter and oviposition sites (Herrington and Larsen 1985, Ramotnik and Scott 1988, Bury et al. 1991). Such retreats have historically insulated *P. idahoensis* from the harsh climate and recurrent wildfires of the northern Rockies (Arno 1980, Nussbaum et al. 1983). As has been proposed for other plethodons (Herrington 1988), we suggest that protection of underground refugia may be the key to preserving populations of this species in the future.

ACKNOWLEDGMENTS

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REPRODUCTION IN THE WESTERN CORAL SNAKE, *MICRUROIDES EURYXANTHUS* (ELAPIDAE), FROM ARIZONA AND SONORA, MÉXICO

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Key words: reproduction, Micruroides euryxanthus, *western coral snake, Arizona, México.*

The western coral snake, *Micruroides euryxanthus* (Kennicott, 1860), ranges from central Arizona and southwestern New Mexico to southern Sinaloa, México, and occurs from sea level to 1770 m (Stebbins 1985). Information on the biology of this species is in Roze (1974). There are only anecdotal accounts of reproduction in *M. euryxanthus* (Funk 1964, Behler and King 1979, Stebbins 1985, Ernst 1992, Williamson et al. 1994, Rossi and Rossi 1995, Degenhardt et al. 1996). According to Lowe et al. (1986), the *M. euryxanthus* reproductive cycle is tied to summer rains; egg laying occurs in July–August with hatchlings appearing in summer. Shaw (1971) assumed breeding occurred in the spring, with egg deposition in late spring or early summer. Roze (1996) reported that in Sonora, México, oviductal eggs were found in *M. euryxanthus* in the 2nd half of May and the end of July; egg laying stretched from the end of July to September. The purpose of this report is to provide information on reproduction in *M. euryxanthus*.

I report on data from 56 *Micruroides euryxanthus* (35 males, mean snout-vent length [SVL] = 382 mm ± 41.9 *s*, range 320–493 mm; 21 females, mean SVL = 371 mm ± 49.7 s, range 315–497 mm) from Arizona and Sonora, México, in the herpetology collections of the University of Arizona (UAZ), Tucson, and the Natural History Museum of Los Angeles County (LACM), Los Angeles (Appendix). Counts were made of oviductal eggs or enlarged follicles (>3 mm diameter). The left testis, epididymis, and vas deferens and part of the kidney were removed from males; the left ovary was removed from females for histological examination. Tissues were embedded in paraffin and cut into sections at 5 μm. Slides were stained with Harris' hematoxylin followed by eosin counterstain. Testes slides were examined to determine the stage of the male cycle; epididymides and vasa deferentia were examined for sperm. Slides of kidney sexual segments were examined for secretory activity. Ovary slides were examined for the presence of yolk deposition.

Data on the male *Micruroides euryxanthus* testicular cycle are presented in Table 1. Testicular histology was similar to that reported by Goldberg and Parker (1975) for the colubrid snakes *Masticophis taeniatus* and *Pituophis melanoleucus*. In the regressed testes seminiferous tubules contained spermatogonia and Sertoli cells. In recrudescence there was renewal of spermatogenic cells characterized by spermatogonial divisions; primary and secondary spermatocytes and spermatids may have been present. In spermiogenesis metamorphosing spermatids and mature sperm were present. Males undergoing spermiogenesis were found in all months examined (April–November; Table 1). Epididymides and vasa deferentia of spermiogenic males contained sperm. The smallest spermiogenic male measured 320 mm SVL. Only 2 males with regressed testes were found, 1 each in June (493 mm SVL) and August (330 mm SVL). No males with recrudescent testes were noted. The sexual segment of the kidney was enlarged and contained densely staining secretory granules in spermiogenic males. Mating coincides with hypertrophy of the kidney sexual segment (Saint Girons 1982).

The smallest reproductively active female (enlarging eggs) measured 356 mm SVL. To

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TABLE 1. Monthly distribution of conditions in seasonal testicular cycle of *Micruroides euryxanthus*. Values shown are the numbers of males with testes exhibiting each of the 2 conditions; none were in recrudescence.

Month	*N*	Regressed	Spermiogenesis
April	1	0	1
May	3	0	3
June	3	1	2
July	2	0	2
August	11	1	10
September	9	0	9
October	5	0	5
November	1	0	1

avoid the possibility of using immature females, I included only *Micruroides euryxanthus* of this size or larger in my analysis of the female reproductive cycle. One female from 31 May (356 mm SVL) contained 3 enlarging eggs (4–5 mm diameter). One female (440 mm SVL) from 23 June contained 6 oviductal eggs (6–7 mm diameter) which may represent the largest published clutch size for this species. Two females, 1 from 30 May (497 mm SVL) and 1 from 13 July (357 mm SVL), contained follicles in early vitellogenesis (yolk granules present). The other females examined were not reproductively active. This included 1 female from May (374 mm SVL), 1 from June (370 mm SVL), 1 from July (386 mm SVL), 2 from September (SVLs 381 mm, 393 mm), 2 from October (SVLs 363 mm, 493 mm). Funk (1964) reported 2 oviductal eggs in a single *M. euryxanthus* from Pima County, Arizona, collected 20 July. Stebbins (1985), Williamson et al. (1994), Rossi and Rossi (1995), and Degenhardt et al. (1996) reported that clutches contained 2–3 eggs. My female sample size is too small to speculate on what proportion of the female population produces eggs each year. However, my finding of 1 May and 1 June females with inactive ovaries may suggest that not all females reproduce annually. The female from July with inactive ovaries (no yolk deposition) may have already deposited eggs. It will be necessary to examine more female *M. euryxanthus* before a conclusive statement can be made. Quinn (1979) found oviductal eggs in only 2/74 (3%) female *Micrurus fulvius tener* from Texas. Only a portion of the female population breeds in other snakes from the North American desert (Goldberg 1995a, 1995b, 1995c, 1996, 1997).

My limited data on the *Micruroides euryxanthus* ovarian cycle appear compatible with the time frame for egg laying suggested by Lowe et al. (1986) for Arizona (July–August) and Roze (1996) for Sonora, México (end of July to September). Quinn (1979) reported that a few females of the Texas coral snake, *Micrurus fulvius tener*, laid eggs in May but most were deposited in June. September newborn *M. euryxanthus* measured 190–200 mm (total length) and weighed 1.5 g (Lowe et al. 1986).

Spermiogenesis occurred in all months in which testes of *Micruroides euryxanthus* were examined (April–November). This may suggest that spermiogenesis is continuous and that males are capable of breeding throughout the year; this would support Rossi and Rossi (1995), who stated that mating may occur in the fall as well as in spring. Quinn (1979) similarly reported an extended period of spermiogenesis (all months except May, June, and July) in *Micrurus fulvius tener*. The reproductive cycle of *M. euryxanthus* appears to fit into Saint Girons' (1982) category "spermatogenesis of mixed type A," in which there is mating in fall and spring with a long period of spermiogenesis.

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APPENDIX

Specimens examined from herpetology collections at the Natural History Museum of Los Angeles County (LACM) and the University of Arizona (UAZ). **Sonora, México:** LACM 16056, 104325. UAZ 9358, 27079, 35214, 44875–76, 45202–203, 45904. **Arizona, Cochise:** UAZ 14435, 14616, 39679, 39681, 45843, 46378, 46834, 50046. **Gila:** 43287. **Pima:** UAZ 9360, 14429–31, 14433, 14436, 14438–39, 14441–42, 14445–46, 14451, 14618–19, 27075, 29658, 34459, 35829, 36557, 37831, 40874, 42608, 45011, 46420, 47344, 47432, 47484, 48342, 48784. **Pinal:** UAZ 14432, 14434, 14444. **Santa Cruz:** UAZ 39677. **Yavapai:** UAZ 14443, 39669, 45748.

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SPREAD OF *PHALARIS ARUNDINACEA* ADVERSELY IMPACTS THE ENDANGERED PLANT *HOWELLIA AQUATILIS*

Peter Lesica[1]

Key words: exotic, invasion, endangered plant, Phalaris arundinacea, Howellia aquatilis, *natural area, Montana.*

Invasive exotic species are considered one of the primary threats to native communities (Mooney and Drake 1986) and are a major concern to natural areas managers (Bratton 1982, Harty 1986). Exotics often displace native dominants, sometimes altering community function as well as composition (Vitousek et al. 1987). They are also implicated in the decline of rare species, but such cases have rarely been documented for plants (Huenneke and Thomson 1995, Lesica and Shelly 1996). Here I present evidence that *Phalaris arundinacea* L. (reed canarygrass), an aggressive rhizomatous grass with native and exotic genotypes, is gradually displacing native marsh vegetation, including the endangered plant *Howellia aquatilis* Gray.

SPECIES DESCRIPTIONS

Phalaris arundinacea (Poaceae) is a strongly rhizomatous perennial grass. Native to northern Europe and northern North America (Dore and McNeill 1980), it has been cultivated for forage and hay in Europe since at least the early 1800s (Schoth 1929). Much of the *P. arundinacea* now found in North America is thought to be derived from cultivars introduced for agriculture (Dore and McNeill 1980, Apfelbaum and Sams 1987), and many of these cultivars have been selected for vegetative vigor (Alderson and Sharp 1994). *Phalaris arundinacea* forms dense monocultures, up to 2 m high in Montana. It is capable of invading native wetlands, causing declines in native species (Apfelbaum and Sams 1987).

Howellia aquatilis (Campanulaceae) is an annual aquatic plant, dependent on yearly recruitment from the seed bank. Seeds of *H. aquatilis* require an aerobic environment to germinate (Lesica 1992), but plants require an aquatic environment to grow and produce flowers and fruits. Large, temporary declines in abundance occur following years when ponds fail to dry by late summer (Lesica personal observation). Seeds germinate in Montana in the fall, growth begins in the spring, and plants grow up through the water column, producing leaves and flowers at or below the surface. Flower production starts in June and continues until drying occurs, usually late August. *Howellia aquatilis* occurs in ephemeral ponds or the margins of shallow permanent ponds dominated by emergent macrophytes, such as *Equisetum fluviatile* L., *Sium suave* Walt., and the tussock-forming *Carex vesicaria* L. These species do not usually form a closed canopy, and *H. aquatilis* generally grows in the spaces between these taller plants. It is known historically from northern California, western Oregon, western and eastern Washington, northern Idaho, and northwest Montana; however, many of these populations are thought to be extirpated. *Howellia aquatilis* is considered threatened or endangered throughout its range in the Pacific Northwest (Lesica and Shelly 1991) and is listed as threatened under the Federal Endangered Species Act.

STUDY AREA AND METHODS

I conducted my study on The Nature Conservancy's Swan River Oxbow Preserve along the Swan River 5 km south of the town of Swan Lake in Lake County, Montana. *Howellia aquatilis* occurs in marshy areas adjacent to a large oxbow slough. *Phalaris arundinacea* is found throughout many of the wetlands of the preserve, where it likely invaded from plantings on the adjacent Swan Lake National Wildlife Refuge.

Phalaris arundinacea occurs on the edge of 2 shallow bays, ca 100 m apart, of a large river

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oxbow (designated North and South marshes; 47°53′N, 113°51′W; 945 m elevation) that also support colonies of *H. aquatilis.* These colonies experience the same hydrologic regime that controls the sometimes significant annual fluctuations in abundance of *H. aquatilis* (see Lesica 1992) but have different depths and distribution of dominant vegetation. In 1987 I established a permanent post in the center of the *P. arundinacea* colony in the North Marsh. The distance from the center post to the edge of the solid *P. arundinacea* sward was measured for 6 radii at 20° intervals (1 interval was 30°) by a hand-held compass. Measurements were repeated in 1991 and 1996. Data were analyzed by repeated measures analysis of variance, with each radius treated as an independent measure of the growth of the sward. Total area estimates for the 110° portion of the colony in 1987 and 1996 were calculated as the sum of the geometrically derived areas of each arc section.

In 1988 I established 2 permanent transects to monitor the abundance of *H. aquatilis* and *P. arundinacea*: 40 m in the North Marsh and 32 m in the South Marsh. Both transects began in colonies of *P. arundinacea* and extended through *Carex vesicaria–Equisetum fluviatile* marsh that supported colonies of *H. aquatilis.* I used the line intercept method (Mueller-Dombois and Ellenberg 1974) to estimate cover of solid *P. arundinacea* swards and *H. aquatilis.* Clusters of *H. aquatilis* stems were treated as if they were the crowns of shrubs, and the distance overlapped by the line was recorded. When the line crossed a single strand, it was recorded as 1 cm (the minimum distance recorded). Transects were read annually in mid-July from 1988 to 1996.

RESULTS AND DISCUSSION

Phalaris arundinacea colonies consist of a monoculture core area surrounded by a periphery where ramets occur among the marsh dominants, *C. vesicaria*, *E. fluviatile*, and *S. suave.* In the North Marsh cover of *P. arundinacea* increased from 20% to 95% in 9 yr in the 3-m-wide ecotonal zone adjacent to the core area at the beginning of the transect. In this same period canopy cover of *H. aquatilis* declined steadily to near zero. Cover along the entire transect fluctuated but did not show a similar overall declining trend (Fig. 1). *Phalaris arundinacea* was completely absent from the other end of this transect in 1988 but was common by 1996. In the South Marsh cover of *P. arundinacea* remained stable over the course of the study, and there was no apparent change in the canopy cover of *H. aquatilis* in the ecotonal zone.

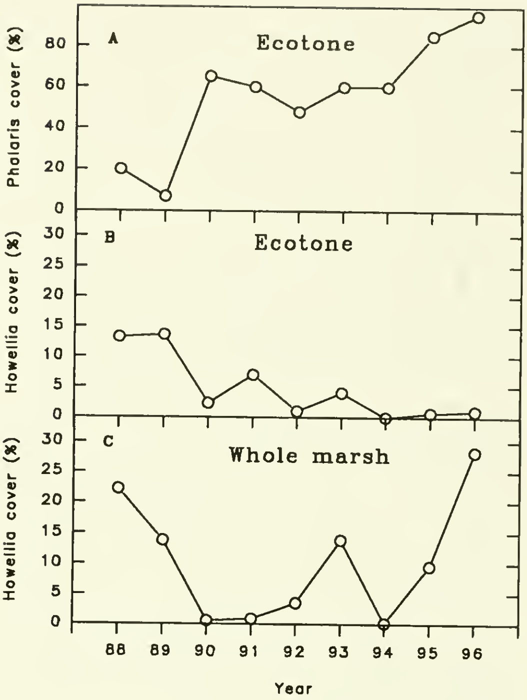

Fig. 1. Percent canopy cover of (A) *Phalaris arundinacea* in the *Phalaris*-marsh ecotone, (B) *H. aquatilis* in the ecotone, and (C) *Howellia aquatilis* in the entire North Marsh from 1988 to 1996.

In the North Marsh the extent of the solid *P. arundinacea* sward intercepted increased for 4 of 6 radii between 1988 and 1996, and this difference was marginally significant ($F_{2,10}$ = 2.86, P = 0.10). The power of this test is limited by the small sample size, so P = 0.10 is a reasonable significance level (Taylor and Gerrodette 1993). The estimated area of the sampled *P. arundinacea* sward was 155 m^2 in 1988 and 209 m^2 in 1996, an increase of 35% in 9 yr.

My study provides indirect evidence that *Howellia aquatilis* is being displaced by *Phalaris arundinacea* in the North Marsh. The size of the *P. arundinacea* monoculture increased in the North Marsh over the course of the study, while the canopy cover of *H. aquatilis* declined to near zero in the area of invasion, even in 1996 when abundance reached a 9-yr high in the entire marsh. The fact that *H. aquatilis* declined in the presence of *P. arundinacea* while increasing elsewhere in the marsh does not prove but strongly suggests interference by *P. arundinacea*.

Phalaris arundinacea forms dense swards that likely produce deeper shade than the more open, native marsh vegetation. Furthermore, *P. arundinacea* monocultures produce deep, continuous, thatch-like litter that decomposes slowly compared to the patchy, quickly decomposing litter produced by the native vegetation. This dense litter layer may inhibit the growth of seedlings (Bergelson 1990), thereby excluding *H. aquatilis*. *Howellia aquatilis* is, however, capable of persisting in mixtures of *P. arundinacea* and native marsh.

Phalaris arundinacea is capable of displacing native wetland vegetation (Apfelbaum and Sams 1987), but the rate of invasion is liable to depend on individual site characteristics. In the North Marsh *P. arundinacea* is increasing at ca 3% per year toward the center as well as around the margins. On the other hand, extent of *P. arundinacea* in the South Marsh did not increase along the transect over the 9 yr of the study.

It is generally acknowledged that *P. arundinacea* is native to the northern portions of North America; however, introduced cultivars are now common throughout much of North America, obscuring the geographic range and habitat of native ecotypes (Anderson 1961, Dore and McNeil 1980). It is generally believed that invasive populations of *P. arundinacea* are derived from nonnative, agricultural cultivars (Apfelbaum and Sams 1987), although the morphological variability of the species makes discrimination between native and nonnative populations impossible (Anderson 1961). Genetic introgression from cultivated into native ecotypes, resulting in more aggressive weeds, has been demonstrated in other species (Baker 1972, Barrett 1983) and may also be occurring in *P. arundinacea*.

Howellia aquatilis is currently known from 7 areas in the Pacific Northwest, and *P. arundinacea* is present at most of these sites. Results of my study, although limited in scope, suggest that this aggressive exotic could reduce populations of *H. aquatilis* throughout much of its range. Although eradication of *P. arundinacea* may not be possible, preventing establishment in uninvaded wetlands and controlling spread in others will be necessary to protect this rare species.

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UTAH REPTILES OCCURRING ONLY IN SOUTHERN UTAH

Wilmer W. Tanner[1]

Key words: reptiles, Utah, Mojave Desert.

In 1935 Dr. Vasco M. Tanner published a list of reptile species that were known to occur in Utah. The list included 40 species, 12 of which were known only from Washington County. A previous study by Woodbury (1931) listed 39 known species for Utah and his recently described subspecies, *Crotalus confluentus concolor.* The Tanner study listed for the first time the worm snake *Leptotyphlops humilis* for Utah, and noted that the southwestern corner of Utah is a habitat distinctly different from other parts of the state. Actually, the southwestern corner is a part of the Mojave Desert, and the reptile fauna extends from this corner of Utah southwest into the deserts of Arizona, Nevada, and California. Both the Woodbury and Tanner reports list probable species that may occur in southern Utah. Tanner lists *Diposaurus d. dorsalis, Uta graciosa, Heterodon nasicus, Micrurus euryxanthus,* and *Kinosternon flavescens.* Both list *Holbrookia maculata approximaris,* but there is still some doubt that it occurs in southeastern Utah. In spite of collecting done since these reports were published, none of Woodbury's or Tanner's probable species have been found in the state.

Since these early lists were published, many reptile specimens have been added to collections, including 7 to be added to the Utah list:

Xantusia vigilis Baird. Collected by Margaret Starey 1940, near Castle Cliff, Beaver Dam slope, Washington County, Utah.

Arizona elegans eburnata Klauber 1946. Collected by L.M. Klauber near St. George, Utah.

Crotalus scutulatus Kennicott 1947. Collected by A.M. Woodbury on Beaver Dam slope.

Crotalus miltchelli pyrrhus Cope 1960. Collected by W.W. Tanner and G.W. Robison, west of Castle Rock on Beaver Dam slope.

Arizona elegans philipi Klauber 1964. Collected by W.W. Tanner near Lone Rock, Kane County, Utah.

Trionyx spinifera emoryi Agassiz 1977. Collected by C.Y. Roby and E.C. Loveless near the Virgin River approximately 4 miles north of St. George, Utah.

Phyllorhynchus decurtatus perkinsi Klauber 1995. Collected by Russel Bazette on road 1/2 mile north of Arizona-Utah state line, Beaver Dam slope, Utah.

These species have all entered through the southwestern corner of Utah. *Arizona elegans* and *Xantusia vigilis,* and perhaps others, may have been in Utah for a long time, but not previously observed. The remaining species may be recent entrants. Why new species are entering is explainable on the basis of temperature increases. An examination of Utah climatic records for the past 50 yr (Utah State Weather Station, Logan, Utah) provided by Donald T. Jensen, director, indicates that there has been a slow warming of this desert area in recent years. These records place the slow increase in minimum and not maximum daily temperatures. The new reptile immigrants except for *Trionyx* are all evening or night foragers and would benefit from warmer and perhaps longer warm evenings. The continued expansion of the range by night foragers indicates that we may still be in the realm of postglacial warming (Wells and Jorgenson 1964). Although published temperature records for southeastern Utah are not available, the occurrence of reptile species, such as *Thamnophis cyrtopsis, Elaphe gutlata,* and probably *Holbrookia maculata,* now in the four corners area of Utah, suggests that this area has also been invaded by reptiles from the south and southeast.

---

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Recently, a specimen of *Tantilla p. utahensis* was taken by Dr. Stanley L. Welsh at Granite Creek, Dolores Triangle, near the Utah-Colorado border, and supports the record reported by Tanner (1966) for Colorado. Two other species, *Xantusia vigilis* and *Lampropeltis california*, have extended their range into the upper Colorado Basin. Thus, even within Utah, desert reptiles seemingly are expanding their ranges; and those requiring a more mesic habitat, such as *Charina bottae* and *Lampropeltis pyromelana*, have been restricted to the mountain habitats.

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BOOK REVIEW

Birds of Zion National Park and Vicinity. Roland H. Wauer. Utah State University Press, Logan, UT 84322-7800. 1997. $14.95, softcover.

Birds of Zion National Park and Vicinity is a revised edition of the booklet by the same name published in 1965 by Roland Wauer and Dennis L. Carter. Whereas the first edition contained references to 233 bird species, this new version contains an annotated list of 252 fully accepted species plus another 35 not fully verified.

While retaining Howard Rollin's colorful full-page paintings of birds associated with 4 of Zion's principal bird communities, this edition is enhanced by 34 pen-and-ink sketches of birds by Mimi Hoope Wolf. Eight color photographs characterize typical Zion National Park scenery, although a picture of the Virgin River with associated vegetation would have been preferable to the one depicting a riparian community where no water is visible.

The book is appropriately dedicated to Jerome Gifford, who kept volumes of meticulous records of all birds in the vicinity of Zion National Park for a number of years. There is hardly a notation to any bird listed therein without some reference to his records. Unfortunately, Jerome died in 1988 before his records could be published. As Dr. William Behle mentioned in the book's foreword, Mr. Wauer "has very successfully incorporated all of Jerome's outstanding records into this new book."

A useful map of the park and surrounding vicinity at the beginning of the book shows numbered locations to which the reader can refer when visualizing where any given bird can be observed. This is especially important to a visiting birder inasmuch as many of these sites can be reached only by trails shown on the map. Locations such as Carpenter Hill, Maloney Hill, and Grafton are referred to as places to find Band-tailed Pigeons, Bushtits, and Song Sparrows, respectively. However, it is somewhat disconcerting to discover that these locations are not listed on the map. When referring to the map, the reader, or visiting birder, must understand that lacustrine habitats such as Kolob Reservoir, Blue Springs Lake, and Grafton Ponds are located outside the park boundaries. Yet many significant sightings, especially of shorebirds, have occurred at these sites and are referenced in the book as part of the park's "vicinity." In addition, Grafton Ponds are actually water treatment ponds that are fenced and generally inaccessible to the general public, a fact not mentioned by the author. (Jerome had a key to the gate.)

One of the most worthwhile contributions by the author is that he lists resident and migratory birds by the habitat in which they are most likely to be found, and then indicates the best time of year for observing them. If the visitor is limited for time and wishes to maximize the birding experience, this information is invaluable; i.e., "More birds may be found . . . in the late spring and early summer than at any other time of the year."

It is gratifying to note that Mr. Wauer has utilized the extensive information gathered from 25 Christmas bird counts (CBCs) in the park; this writer was privileged to participate in many of them. With only 1 exception (Steller's Jay), high and low numbers are listed for each species observed on the CBC as well as the number of years any given species has occurred. It is this attention to detail that makes this much more than just a dust-gathering book for the library shelf.

The following statements regarding species abundance are instructive: "This is the most commonly seen owl in the Zion Park area" (Great Horned Owl). "This is one of Zion's most characteristic summer birds" (White-throated Swift). "This is one of Zion's most characteristic birds" (Western Wood Pewee). "No other bird is so representative of the Zion Park area" (Canyon Wren). "This is one of the park's most wide-ranging songbirds and is present at all elevations and habitats" (Solitary Vireo). "This is one of Zion Canyon's most numerous and obvious songbirds in summer" (Black-headed Grosbeak).

In addition to Jerome's records and the CBC data, the author gained firsthand experience by banding almost 6000 birds during the more than 3 yr he spent in the park. Many sightings of the birds of Zion, and for that matter southern Utah, are the results of Mr. Wauer's commitment to keeping complete and accurate records. In addition, he utilized nesting records from various observers including his own. An outstanding contribution of this book is that it demonstrates the importance of keeping complete and accurate records.

Birds of Zion National Park and Vicinity has contributed significantly to our understanding of the distribution and abundance of bird species within and around one of the most beautiful national parks in this country. The author is to be commended for his efforts in making this information available.

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THE

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